The breeding biology and ecology of the White-necked Picathartes *Picathartes gymnocephalus* temminck 1825, in Sierra Leone

Thesis

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THE BREEDING BIOLOGY AND ECOLOGY OF THE WHITE-NECKED PICATHARTES *PICATHARTES GYMNOCEPHALUS* TEMMINCK 1825, IN SIERRA LEONE

HAZELL SHOKELLU THOMPSON

Thesis submitted for the degree of Doctor of Philosophy, Open University

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Royal Society for the Protection of Birds (Sponsoring Establishment) in collaboration with The University of Edinburgh

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ABSTRACT

This thesis investigates the ecology, taxonomic affinities and conservation management in Sierra Leone of a threatened West African forest bird, the White-necked Picathartes *Picathartes gymnocephalus*, which has not been previously studied in detail.

The incubation and nestling periods (20 and 25 days) respectively were longer than is usual for most tropical passerines. In most cases, one clutch of two eggs was laid between June and December, immediately followed by moult between January and May (the dry season). Peaks in egg laying occurred 1-2 months after the maximum monthly rainfall. Both parents cared for the young and fed nestlings disproportionately more earthworms, frogs, millipedes and earwigs in relation to their abundance in the environment. Nestlings fledged when still as much as 30% below adult size.

Food abundance peaked in both forest and farmbush (forest regrowth) habitat at the start of the wet season and in the early part of the dry season; coinciding with the period immediately prior to egg-laying and with dispersing fledglings respectively. Potential *Picathartes* prey were more abundant in farmbush than forest habitat.

The proportion of eggs laid that resulted in fledged young was 22.9% and productivity was 0.22 chicks per adult. Nest predation was the main cause of nest failure but infanticidal behaviour played a significant role. A substantial number of non-breeding birds were apparently present in populations and infanticidal behaviour may have been a consequence of competition for limited nest sites.

Population density was estimated as 0.37 individuals km^{-2} and the total population in Sierra Leone as about 1100. Local populations in forest reserves are close to the theoretical minimum for long-term viability in all cases but populations are apparently stable or declining only very slowly. Abandonment of colonies was associated with habitat degradation but there was also evidence that *Picathartes* may be fairly tolerant to disturbance in some areas.

Phylogenetic analysis using mitochondrial DNA of the cytochrome *b* gene suggests that *Picathartes* is more closely related to the thrush-babbler assemblage than the crows.

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The individuals and organisations mentioned in this section made the production of this thesis possible. My sincere thanks to all of them. My apologies (and thanks also) to anyone omitted, who helped in any way during the study.

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Numerous village chiefs in various parts of the country, allowed *Picathartes* surveys in their territories. Special mention must be made of the chief of Baiama in the Kenema district who played host to the *Picathartes* team in the Kambui Hills for several weeks. Many local people led us to *Picathartes* nesting sites or in a few cases to nests of swallows.

In the UK, Catriona MacCallum showed me the ropes at the University of Edinburgh, and Yvonne Edwards plugged me in to the Human Genome Project Resource Centre in Cambridge. Claire Grant was the ideal landlady.

Valerie, Vanessa and recently, Olumide, provided the love, support and stability which has kept me going all these years.

This thesis is dedicated to the memory of my mum - Mrs Ruby Thompson, and Dad - Mr. Benjamin Thompson.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1. OVERVIEW

This thesis deals with research carried out to gain a better understanding of the ecology of a threatened West African forest bird species - the White-necked Picathartes *Picathartes gymnocephalus*. *P. gymnocephalus* is an avian oddity whose systematic position is unclear and of whose general ecology very little is known. The species is restricted to five countries in West Africa, and is regarded as declining throughout its range, but no recent data are available. It is classified as vulnerable in the African Red Data Book of threatened species (Collar *et al*, 1994).

The overall aim of the study was to investigate those aspects of *gymnocephalus* ecology which were relatively uncommon among other tropical forest birds whilst at the same time generating useful information for the species' conservation. In view of such a remit and the interruptions to field work occassioned by a civil war (see Chapter Two), the study was wide-ranging and in consequence had to be superficial in places.

1.2. BACKGROUND INFORMATION ON *PICATHARTES*

1.2.1. Distribution

The genus *Picathartes* comprises two species - the White-necked Picathartes, *P. gymnocephalus* and the Grey-necked Picathartes, *P. oreas*, both of which are restricted to the rain forests of West and Central Africa. *P. gymnocephalus* occurs in Guinea, Sierra Leone, Liberia, Cote d'Ivoire and Ghana (Collar and Stuart, 1985; Hayman *et al*, 1994; Collar *et al*, 1994) whilst *P. oreas* has been recorded from southeastern Nigeria, southwest Cameroon, north and central Gabon, continental

Equatorial Guinea and Bioko (Fig. 1.1)(Collar and Stuart, 1985; Butynski and Koster, 1989; Collar *et al,* 1994).

1.2.2. Identification

Picathartes are 200 - 250g birds which are sexually monomorphic. Both species have: a bare brightly coloured head (yellow in *gymnocephalus*, crimson and powder blue in *oreas*); black parietal patches; a disproportionately large crow-like black bill; a relatively long neck and tail; long silver - grey legs and a general plumage appearance of grey-brown above and whitish below (Plate 1.1.).

1.2.3. Ecology

Little is known of the behaviour, social organisation and ecology of *Picathartes*. Accounts in the literature are brief and largely anecdotal (see Collar and Stuart, 1985). These records suggest that the two species occur most often in rocky, hilly terrain in rainforest, spending most of their time on the ground or close to it (Webb, 1949; Serle 1952b; Glanville, 1954; Attenborough, 1955; Grimes and Gardiner, 1963; Brosset, 1965a, b; Grimes and Darku, 1968; Golding, 1968; Moore, 1974; Tye, 1987; Fotso, 1993). Walker (1939) found *P.gymnocephalus* foraging at army ant columns. Willis (1983) found that strong ant following in *Picathartes* contrasted strongly with the limited role of other ant-following families of birds in Africa (Babblers-Timaliidae and Shrikes-Laniidae).

Army ants (Dorylinae) raid for food in groups and change their nest site periodically (Willis & Oniki, 1978). They are a characteristic feature of African and neotropical rainforests which provide a food resource of varying importance to several bird species. These bird species follow marching swarms to capture arthropods flushed by the ants (Willis & Oniki, 1978). The foraging behaviour of these ant-following birds is well-documented (Willis and Oniki, 1978; Willis, 1983; Coates-Estrada and Estrada; 1989), but their diets have not been analyzed in detail (Chesser, 1995) and few quantitative data exist (Coates-Estrada & Estrada, 1989). This study includes an

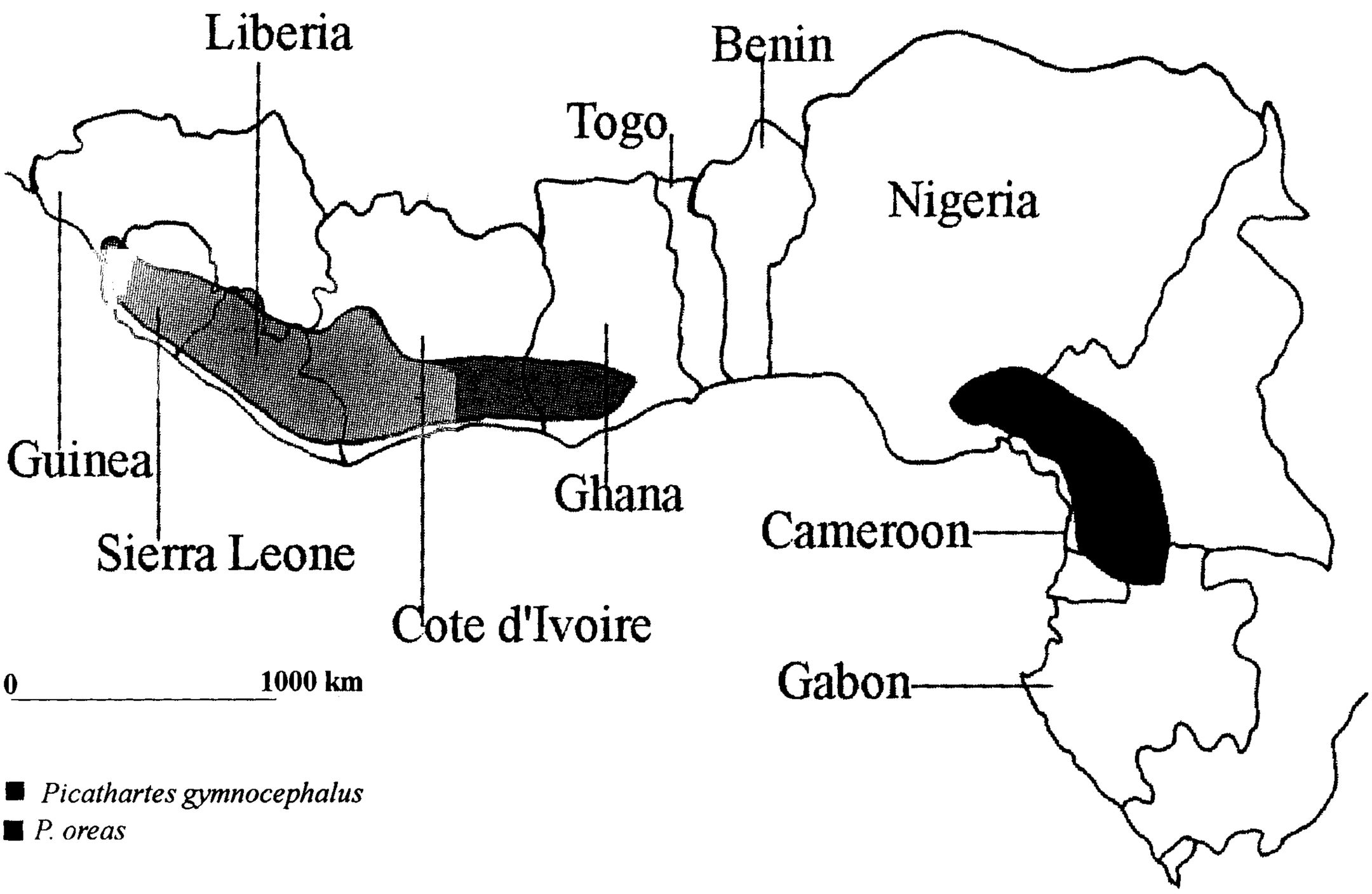


Fig. 1.1. The geographical ranges of *Picathartes gymnocephalus* and *P.oreas*

Plate 1. Adult *Picathartes gymnocephalus* feeding nestling

analysis of the diet of *P. gymnocephalus*. The results should therefore extend considerably our basic knowledge of the ecology of an ant-following bird species in Africa.

The two species of *Picathartes* breed in mud nests on rock or cliff faces and/or cave roofs in colonies of 1-40, under a rain forest cover (pers. obs.). This uncommon breeding behaviour has been little studied. Previous investigations have been largely qualitative with few prolonged observations (eg Glanville, 1954; Grimes 1963; Grimes and Gardiner 1963, Brosset 1965a, 1965b), and have not covered the whole breeding cycle (Tye, 1987; Fotso, 1992). However, although nothing definite was known, Brosset (1965a) and Grimes (1976) suggested that *Picathartes* was a cooperative breeder, with the whole colony assisting in incubation and the rearing of the young (Brosset 1965a, b, Grimes 1976).

Cooperative breeding as a social system is defined primarily by the regular involvement of helpers in the feeding and care of the young (Brown,1978, 1987; Emlen, 1991, 1997). Cooperatively breeding species tend to live in small relatively stable units (2-20 members), with communally defended, all-purpose territories which they rarely leave (Brown 1978, 1987). In contrast, colonial species congregate temporarily at concentrations of food or at restricted nest sites, but the groups formed are temporally unstable. The foraging area of the colony is usually undefended but individual nests are commonly defended at some stage (Brown 1978). Helping is known in several colonial species (Koenig *et al*, 1992) but in most colonial species helping is considered exceptional (Brown 1978, 1987, Du Plessis *et al*, 1995). *Picathartes* therefore apparently offered the opportunity to investigate an uncommon phenomenon (cooperative breeding in a colonial species) in a poorly studied avifaunal environment (African rainforest).

Du Plessis *et al* (1995) noted that a bias is frequently introduced into conceptual reviews of avian biology and behaviour by the lack of information on poorly-studied avifaunas such as African rainforests. Any reliable data on such avifaunas are therefore probably valuable in themselves. Moreover, cooperative breeding lends

itself very well to field tests of ideas about inclusive fitness, altruism. and kin selection (Brown, 1978, 1987; Emlen. 1991. 1997). These considerations were powerful incentives for starting an autecological study of *Picathartes.*

The original plan was to collect information on the basic biology of *Picathartes* (Chapter 3), then use this information to formulate more specific research questions. I thought *Picathartes* colonies would be particularly well-suited to investigations on genetic relatedness between breeding unit members in a colony. This could have been an excellent testing ground for evolutionary predictions of the costs and benefits of living within colonies and family kin groups (Emlen 1991; see Emlen 1997 for recent review). In the event, disruptions to field work by civil war prevented collection of sufficient blood samples and the intensive observations of marked individuals required for this type of study, and field work had to be modified accordingly. A collaborative study on taxonomy (Chapter 7) was substituted in this area.

1.2.4. Taxonomic relationships

The systematic position of *Picathartes* is still unclear and has been the subject of some controversy. The genus has been variously placed in the Corvidae (Serle, 1952; Sibley and Munroe, 1990); the Sturnidae or close to it (Lowe, 1938; Bannerman, 1948,1951); the Muscicapidae (Deignan, 1964); the Timaliidae (Delacour and Amadon, 1951; Hall and Moreau, 1970; Sibley, 1973, 1988; Olson,1979; Sibley *et al,* 1988; Dowsett and Forbes-Watson, 1993; Dowsett and Dowsett-Lemaire, 1993) and the Sylviidae (Sibley *et al*, 1988). The taxonomic rank at which the two species are classified has also varied; from separate family status (eg Picathartidae, Bannerman 1951; Sibley and Munroe 1990) to sub-family (eg Picathartinae, Deignan 1964); tribe and sub-tribe (eg Picathartinii, Sibley *et al*,1988).

The uncertainty of the taxonomic position of *Picathartes* has generated a concurrent problem of determining the nearest relative of the genus. Several genera, mainly belonging to the Sturnidae and Timaliidae, have been accorded this status, most notably, the starlings and mynahs of the Phillipines and New Guinea - *Sarcops*, *Mino*

and *Eulabes* (Lowe 1938); *Eupetes,* the Malay Rail Babbler of southeast Asia (Serle, 1952a; Olson, 1979); babblers of the genus *Turdoides* (Sibley, 1970,) and most recently, the South African Rockjumper *Chaetops* (Sibley and Munroe, 1990). The problem is still unresolved. Blood samples collected from *Picathartes* in this study were therefore used to investigate the taxonomic relationships of the genus through DNA sequence analysis (Chapter 7).

1.2.5. Conservation status

The two species of *Picathartes* are classified as vulnerable under the IUCN (1994) international criteria for threatened species (Collar *et al*, 1994) and are listed on Appendix I of CITES. In addition, they are protected by national law in some of the range states (Cameroon, Ghana and Sierra Leone).

1.2.6. Population

Picathartes populations are thought to be small, fragmented and declining (Collar *et al,* 1994), but this assessment is almost wholly based on anecdotal accounts and guesswork (see Collar and Stuart 1985 for a review). These impressions are almost certainly enhanced by the secretive behaviour of the species, the inaccessibility of its usual habitat (see Section 1.2.3.) and the fact that there have not been any previous specific surveys to determine distribution and population density. Such information is essential if any plans to conserve the species are to succeed. In this study, a country-wide survey for *gymnocephalus* breeding sites was carried out throughout Sierra Leone (Chapter 6). This is the first attempt at determining the distribution and estimating the population of the species in any range state. The information is likely to prove especially useful to the Gola Rain Forest Conservation Project, initiated in Sierra Leone in 1990 for the sustainable management of the Gola forests, the largest remaining lowland rainforest in the country.

1.2.7. Threats

The main threats to *Picathartes* populations have been collection for export to western zoos and habitat loss. Collection for zoos probably contributed greatly to the depletion of wild populations between 1955 (when the first specimen was exhibited alive outside Africa in London Zoo) and the early 1980s. Very high captive mortality rates (most birds died within 24 hours) engendered disturbance and destruction of many colonies (W. Gatter cited by Stuart and Collar, 1985; pers. comm. with local people). Captive breeding of the two *Picathartes* species has not been very successful with successful breeding occurring in only four of 24 zoos in two decades (Faust, 1971; Dekker, 1971, 1973; McKelvey 1981).

Collection for zoos from wild populations has now virtually ceased so that the prime threat to populations is probably the clearing of forests during logging operations and for farming. There are no records of the birds surviving in areas where the forest has been destroyed.

Opportunistic hunting and trapping occurs throughout the birds' range (Collar *et al*, 1994) but this is probably a minor threat as the birds are considered of little food value (pers. obs.).

1.3. AIMS

The specific aims of the study were:

1. to describe the breeding biology of *Picathartes gymnocephalus*
2. to examine seasonal variation in food and rainfall and how such variation might influence *gymnocephalus* reproductive activity
3. to estimate distribution and population density of the species throughout the country
4. to determine genetic relationships within and between colonies

The unifying theme of these various aspects of the study was the need to discover those aspects of the ecology and behaviour of the species which are critical to its

conservation and to make recommendations for its long-term survival. However, the investigation of genetic relationships at breeding colonies was later modified to an investigation of the taxonomic relation ships of the genus (see Chapter 2).

1.4. JUSTIFICATION AND STRUCTURE OF THE THESIS

Describing the breeding biology of a species (Chapter 3) is a step towards understanding its behavioural ecology and is essential in any attempt to formulate conservation policy beneficial to the species. Here, emphasis was placed on determining levels of breeding success in *gymnocephalus* populations and identifying the major factors influencing these levels. This information should provide an insight into *gymnocephalus* population dynamics and the species prospects for long-term survival.

On a more general scale, the patterns of avian breeding dynamics in the tropics have been little studied (Dowsett-Lemaire, 1985). Furthermore, Karr (1990a) notes that tropical forest avifaunas present a bewildering array of natural histories, many of which are only now beginning to be understood. Clarification of the pattern and process that accounts for the attributes of tropical forest bird communities depends on a clearer understanding of these natural histories.

In tropical rain forests, temperature fluctuations are minor as are annual changes in photoperiod. Rainfall is therefore usually the key environmental factor which modifies the physical environment (Richards, 1952; Owen, 1969; Wolda, 1978a; Boinski and Fowler, 1989; Keast, 1990). Fluctuations in rainfall impose a high degree of seasonality which changes resource availability for both plants and animals (Fogden, 1972; Janzen & Schoener, 1968; Frith and Frith, 1990). Despite this realization, data on the seasonal patterns in variation of African ecosystems are scarce (Dingle and Khamala, 1972; Wolda, 1978b; Critchley *et al,* 1979; Boinski and Fowler, 1989; Frith and Frith, 1990). In Chapter Four, data are provided on seasonal variations in the abundance and diversity of undergrowth fauna in an African forest. These organisms comprise a large part of the known diet of *Picathartes* (see Chapter

Five). The variations in faunal abundance and data on rainfall seasonality are then examined in relation to the timing of breeding and moult in *P. gymnocephalus*. This should allow the annual cycle of *gymnocephalus* to be interpreted in terms of resource seasonality.

The relationship between reproductive and moult cycles in birds, and rainfall seasonality has been studied extensively in the tropics (Moreau, 1950; Skutch, 1950; Snow and Snow, 1964; Fogden, 1972; Diamond, 1974; Stiles, 1980; Serle, 1981; Brosset, 1981; Dowsett and Dowsett-Lemaire, 1984; Dittami and Knauer, 1986; Thompson,1987; Jones, 1989a; Akinpelu, 1994), but studies relating breeding activity to temporal variation in the abundance of food resources have been mainly carried out in the neo-tropics (eg Ward, 1969; Worthington, 1982; Poulin *et al*, 1992; Young, 1994; Tye, 1996) and are extremely scarce for African forests (Keast, 1985; Karr 1990). Chapter Four provides information on the relation of the annual cycle of a little-known African rainforest species to food and rainfall seasonality in the African environment.

Also in Chapter Four, the abundance and diversity of the soil fauna in the forest around *gymnocephalus* breeding sites are compared with that in adjacent farmbush areas. Farmbush is vegetation derived from cleared mature forest, which comprises a thicket of climbers, shrubs, young saplings and razor grass (*Sceleria barteri*) in about two to five years after clearing and eventually grades into secondary forest in 20-30 years (Cole, 1968). The results of this comparison, although preliminary, should throw some light on the potential effects of deforestation on the ecology of *gymnocephalus* and other ground-storey rainforest birds with similar diets.

In Chapter Five, the results of a detailed analysis of the diet of breeding adult *gymnocephalus* and their nestlings are described. The diet of *gymnocephalus* has not previously been analyzed in detail. Several authors have occasionally presented dietary data but these have either been derived from brief visual observations (McArdle. 1958; Grimes, 1963; Willis, 1983) or from stomach contents of one or two individual birds (Walker 1939). Previous information on the diet of *P.oreas* is

similarly scanty, consisting largely of brief qualitative statements (Lowe 1938, Brosset and Erard, 1986) except that Tye (1987) quantified visual observations of parental feeding trips to a nest of two nestlings over five days in Cameroon. This study is therefore the first attempt at a comprehensive description of the diet of *Picathartes*. This information should indicate some of the critical resources on which *Picathartes* depends for survival and continued productivity. Correlation of these data with the ecological variables measured in Chapter Four - rainfall and potential prey availibility - should increase understanding of the influence of tropical forest seasonality on the ecology of *P. gymnocephalus* and other ecologically similar avifauna.

Chapter Six provides information on the distribution and population density of *P. gymnocephalus* in Sierra Leone and quantifies the ecological parameters of colony and nest locations. These data are analysed with a view to assessing the conservation status of *P. gymnocephalus* in Sierra Leone. Such information is essential for the conservation and management of the species.

In Chapter Seven, I use mitochondrial DNA sequences of *Picathartes* to carry out a phylogenetic analysis of the taxonomic relationships of the genus. This has been a long standing problem in avian systematics (see Section 1.2.4.), which the information presented in this chapter should help to clarify.

A discussion is provided at the end of each chapter which highlights the important inferences that can be drawn from the results. These chapter discussions also assess the significance of the results in the context of contemporary knowledge on *Picathartes* and Afrotropical birds in general. Chapter Eight pulls together these individual chapter inferences to make practical recommendations for the conservation and management of the species.

CHAPTER TWO

STUDY SITES AND METHODS

Field work was mainly carried out in Sierra Leone. In addition, a month was spent in Cameroon in order to obtain blood samples for DNA sequence analysis from *Picathartes oreas* and for field observations on that species (see Chapter 6).

2.1. BACKGROUND INFORMATION ON SIERRA LEONE

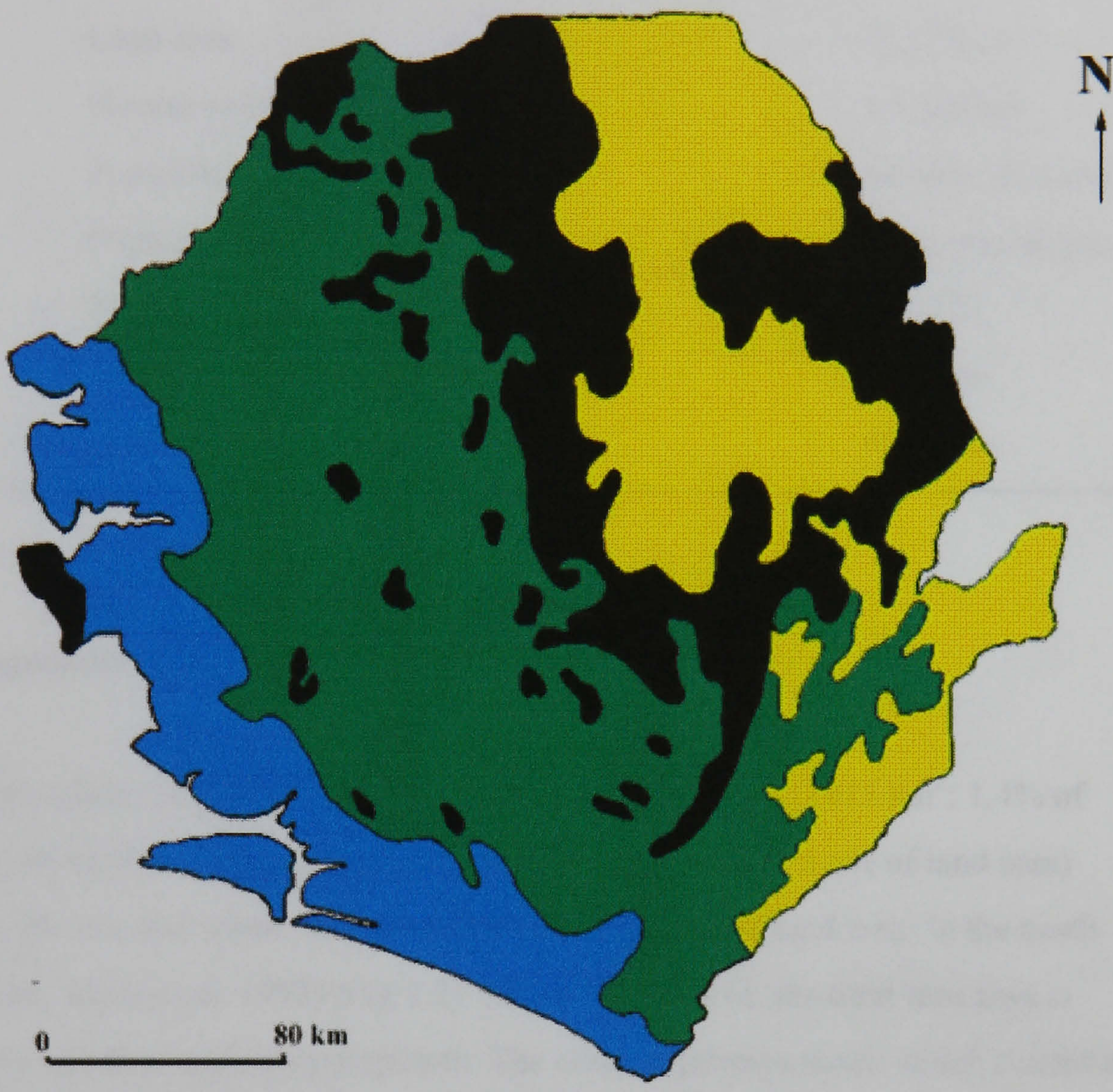
2.1.1. Basic data

Sierra Leone is a coastal West African country on the western edge of the Upper Guinea rain forest belt (6°55'N - 10° 00'N and 10° 14W - 13°17'W) (Fig 1.1, Table 1; see section 2.1.4).

The country has four main topographical regions: coastal lowlands, interior plains, interior plateaux, and scattered mountains and hills (Fig 2.1) (Birchall *et al*, 1979). The interior plains and plateaux constitute two thirds of the land area, and the hills and mountain ranges mainly rise out of this region. The coastal lowlands are 50km wide in the south and 125km wide in the north, but are interrupted by the mountainous Western Area Forest which rises steeply from the sea near Freetown.

A linear escarpment runs from northwest to southeast across the country, effectively separating the coastal lowlands (below the 200m contour) from the higher interior (mostly above 500m). A series of rivers rise from the region of the escarpment and flow roughly parallel to each other in a southwesterly direction to the coast. The interior highlands are topped by two massifs in the northeastern interior - Mt Bintimani in the Loma Mountains (1946m) (the highest peak in sub-saharan Africa west of Mt Cameroon) and Sankan Biriwa (1709m) in the Tingi Hills.

Fig 2.1. The main physical regions of Sierra Leone (based on Gordon *et al*, 1979)



Key

- **Coastal plain**
- **Hills and mountains**
- **Interior plains**
- **Plateaux**

Table 1: Basic data on Sierra Leone

Land area	72,325 km^2
Human population (mid-1991)	4.3 million
Population density	59 individuals/km^2
Population growth rate	3.7 % per annum
Per capita GNP (1991)	US$370
Total forest cover (1992)	5064 km^2
Annual deforestation rate (1981-5)	60 sq.km

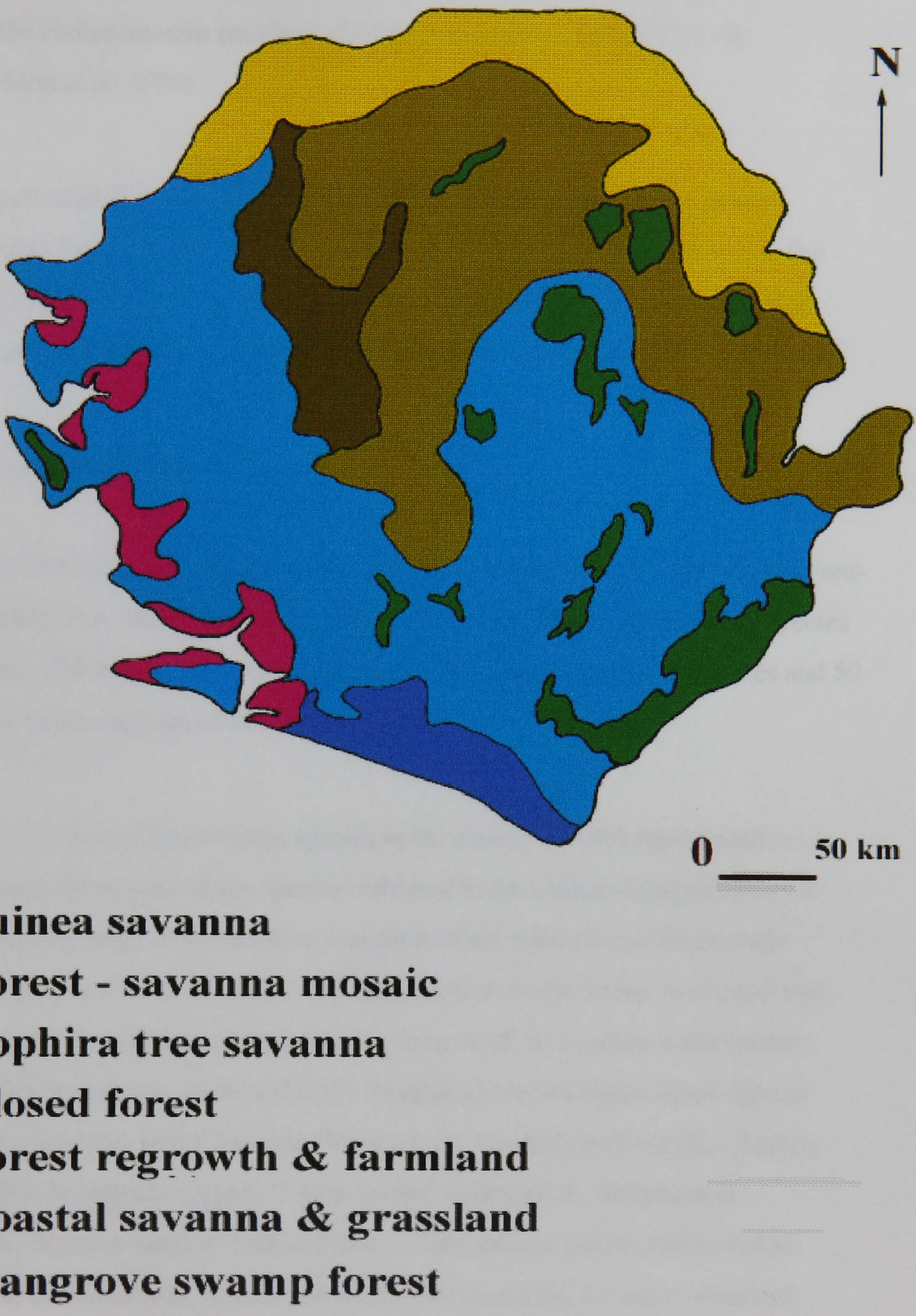
2.1.2. Vegetation

Three main climax vegetation zones occur: coastal mangroves (1015 km^2; 1.4% of land area) along the 425km coastline; closed forest (4006 km^2; 5.6% of land area) mainly in the east and south; and woodland savanna (18% of land area) in the north (Cole, 1968; Sayer *et al*, 1992) (Fig 2.2). About 56 - 60% of the total land area is covered by farmland and forest regrowth. The other vegetation zones which constitute the remaining 10-15% of the land area are: gallery forest along the courses of the main rivers and tributaries, inland swamp forest in valleys and bolilands (seasonally flooded depressions), forest-grassland formations (mainly *Lophira* tree savanna and coastal park savanna) and grassland (Fig 2.2)

2.1.3. Climate

The climate is characterised by fairly high year-round temperatures (mean annual temperature - 27°c) and heavy seasonal rainfall (usually from May - October; mean annual rainfall - 3000mm). Relative humidity averages 80% in the wet season but drops to a mean of about 65% in the dry season (Birchall *et al*, 1979).

Fig 2.2. The main vegetation zones of Sierra Leone (based on Gordon *et al*, 1979)



Diurnal temperature variation is in the region of 9 - 17°C. The highest mean monthly temperatures (32°C - 35.6°C) generally occur in March/April whilst July/August are typically the coolest months (minima of 14°C in the interior and 21°C at the coast)(Gordon *et al*. 1979).

Mean annual rainfall decreases from the south (3000-4000mm) to the north (< 2000mm) and from the coast (4000-5000mm) to the interior (about 3000mm). The area of highest rainfall is the coastal Peninsula Mountains in the southwest where mean annual rainfall is more than 5000mm (Gordon *et al*, 1979).

2.1.4. The avifauna of Sierra Leone

A total of 626 bird species have been recorded in Sierra Leone (Dowsett and Dowsett-Lemaire 1993; P.A. Robertson - pers. comm. 1995, pers. obs.). Of these, 438 species are resident; 138 are regular seasonal migrants, including 92 palearctic species and 50 species are either vagrants or of uncertain status.

There are 172 Guinea forest biome species in the country (61.4% representation). Guinea forest biome species are species restricted to the Guineo-Congolean moist evergreen forest which stretches from Guinea in West Africa to the Democratic Republic of Congo (formerly Zaire) in Central Africa. Sierra Leone is of particular importance for Guinea forest biome species because of its location at the western limits of this forest zone. Eleven globally threatened Guinea biome forest species occur in the country: White-breasted GuineaFowl, *Agelastes meleagrides*; Rufous Fishing Owl, *Scotopelia ussheri*, Yellow-footed Honeyguide, *Melignomon eisentrauti*; Western-wattled Cuckoo Shrike, *Campephaga lobata*; Green-tailed Bristle-bill, *Bledia eximia*; Yellow-throated Olive Greenbul, *Criniger olivaceus*; White-necked Picathartes, *Picathartes gymnocephalus*; Black-headed Stream Warbler, *Bathmocercus cerviniventris*; Sierra Leone Prinia, *Prinia leontica*; Nimba Flycatcher, *Melaenornis annamarulae*; and Gola Malimbe, *Malimbus ballmani*. Eight of these eleven threatened species are endemic to the western half of the Guineo-

Congolean forest (the Upper Guinea Forest) which is seperated from the main Lower Guinea block by the Benin savanna gap. Four of the eleven threatened species (Gola Malimbe, Yellow-footed Honeyguide, Western-wattled Cuckoo-shrike, Nimba Flycatcher) reach the western limit of their range in Sierra Leone. The occurrence of a fifth threatened species (White-breasted Guinea Fowl) further west in Guinea is doubtful (Dowsett and Dowsett-Lemaire 1993).

In addition to its importance for forest species, Sierra Leone is also one of the major stopover sites for Palearctic migrant waders that winter along the West African coast (Tye and Tye, 1987). Sites along the Sierra Leone coast support 130,000 - 200,000 waders with three sites regularly holding more than 20,000 waders each (Tye and Tye 1987; pers. obs.). A near-threatened tern - the Damara Tern, *Sterna balaenarum*, which numbers only one or two thousand pairs in its restricted breeding range on the west coast of southern Africa (Collar *et al,* 1994) reaches the westernmost extremity of its known range in Sierra Leone (Thompson in Taylor and Rose, 1994).

2.1.5. Other fauna

The 178 known mammal species in Sierra Leone include 15 non-human primates (six of which are globally threatened), 18 antelope species (16 threatened), nine species of fruit bats (of which one - *Epomops buettikoferi* is endemic to West African forests), and relict African Elephant (*Loxodonta africana cyclotis*), Leopard (*Panthera pardus*), Pygmy Hippopotamus (*Cheoropsis liberiensis*) and Manatee (*Trichechus senegalensis*) populations. Other animal species of conservation concern include all three West African crocodiles, two endemic amphibians (*Cardioglossus aureoli* and *Bufo cristiglans*) and two endemic dragonfly species - *Argiagron leoninum* and *Allorhizucha campioni*.

2.1.6. Flora

The country's flora comprises at least 2000 species of plants, 74 of which (including one genus) are endemic (Cole 1968, Stuart and Adams, 1990).

2.1.7. Biodiversity conservation

There are six categories of legally protected areas in Sierra Leone. In these areas, protection is provided to flora and fauna on a sliding scale from Strict Nature Reserve (excellent protection; no human activity allowed) through National Park, Game Reserve, Game Sanctuary and Non-hunting Reserve to Forest Reserve (licensed exploitation; no protection to fauna). Presently, there are 29 forest reserves, four non-hunting reserves, one game sanctuary and one national park in the country.

Twelve groups of birds (in taxa ranging from species to families) and 16 groups of mammals and reptiles are legally protected. *Picathartes gymnocephalus* has the best possible protection. It is a prohibited animal, which means killing and trapping of adults and young is illegal but there is little or no awareness of its conservation status.

2.2. STUDY SITES

2.2.1. Geography of the study sites

The main study sites were in the Western Area Peninsula Forest (WAPF)(8° 15'; 13° 15'W), the Gola forest reserve (7° 40'N, 10° 45'W) and the Kambui Hills forest reserve (7° 45'N, 11° 15'W) (Fig 2.3).

The WAPF comprises a forested range of hills (177 km^2) located three to five kilometres from the western Atlantic coast of Sierra Leone (Figs 2.3 and 2.4)

The Kambui Hills forest reserve (158 km^2) is situated about 320km inland from the WAPF between the towns of Blama and Kenema on the southwest edge of the interior plateau region (Figs 2.3 and 2.5).

Gola forest (located 50 km east of the Kambui Hills) is the largest remaining tract of lowland closed canopy forest in Sierra Leone and is divided into three sections: Gola North - 458 km^2 , Gola East - 228 km^2 and Gola West 62 km^2 . Gola North and East abut the Sierra Leone/Liberia border in the eastern province (and continue into Liberia as the Loffa-Mano forest). Gola West is separated from Gola East by the Mahoi river (Fig 2.6). Settlements and non-forested land separate Gola East from Gola North.

The terrain in the three areas is dominated by rugged extensive rolling hills (up to 900m a.s.l in the WAPF), isolated rocky outcrops and narrow steep-sided valleys. Steep slopes (15 - 30°) are common, rising to 45° in some parts of Gola North. Numerous rocky, mainly seasonally flowing streams drain the hills in each reserve, although to a lesser extent in the Kambui Hills than the other two reserves. Gola West is an exception to this general topography and is mainly low-lying and swampy (<150m) with few hills.

2.2.2. The vegetation at the study sites

The vegetation in the interior of the reserves is essentially lowland evergreen rain-forest of the *Lophira/Heriteria* tree community complex (Cole 1968, 1996; Davies, 1987; Iles *et al*, 1993). Common species such as *Heriteria utilis, Uapaca guineensis, Cryptosepalum tetraphyllum, Piptadeniastrum africanum and Cynometra leonensis* form a main canopy at 15-20m over a sparse and open understorey. Emergent trees (*Lophira* spp, *Parkia bicolor, Parinari excelsa, Erythrophleum ivorense* and *Klainedoxa gabonensis*) reach maximum heights of 50-60m. Deciduous species (eg. *Terminalia* spp, *Daniella thurifera* and *Anthonotha fragrans*) also occur but in fairly low proportions. Tangled undergrowth dominated by *Sceleria barteri*

develops in the vicinity of tree fall gaps. On bare rocky slopes and hill summits, low scrub is the climax vegetation.

Continuous forest cover at the centre of the reserves and on steeper, less accessible slopes is interrupted on lower-lying land by secondary forest (ie forest in which past or present human activity is detectable) which grades into forest/farm re-growth mosaic close to the reserve boundaries (within 1 - 2 km). Common secondary forest tree species include *Musanga cercropioides, Funtumia africana, Carapa procera* and *Myrianthes arborens* (Savill and Fox, 1967). In the WAPF, the forest gives way to natural grassland on laterite plains at the foot of the hills. This grades into mangroves along the coast and becomes farmland and forest regrowth with small remnants of *Lophira* savanna inland.

2.2.3. Geology

The WAPF hills are formed from an intrusive body of rock along the Atlantic coast known as the Freetown Igneous Complex and is a layered complex of gabbro, norite, troctolite, and anorthosite (Gordon *et al*, 1979).

Ancient crystalline rocks of the Pre-Cambrian period underlie the Gola and Kambui Hills reserves as it does in most of Sierra Leone (Birchall *et al*, 1979). The soil is derived from a widespread granite/greenstone complex. Ores of chromium, gold, iron and magnesium are located in strips of metamorphic rock that permeate the dominating granite (Iles *et al,* 1993). In the Kambui Hills, the complex comprises a series of iron and magnesium-rich rocks over a quartz-rich basement of granitic composition. (Birchall *et al*,1979).

Fig 2.3. Map of Sierra Leone showing the *Picathartes gymnocephalus* study sites: 1 = WAPF; 2 = Kambui Hills and 3 = Gola Forest.

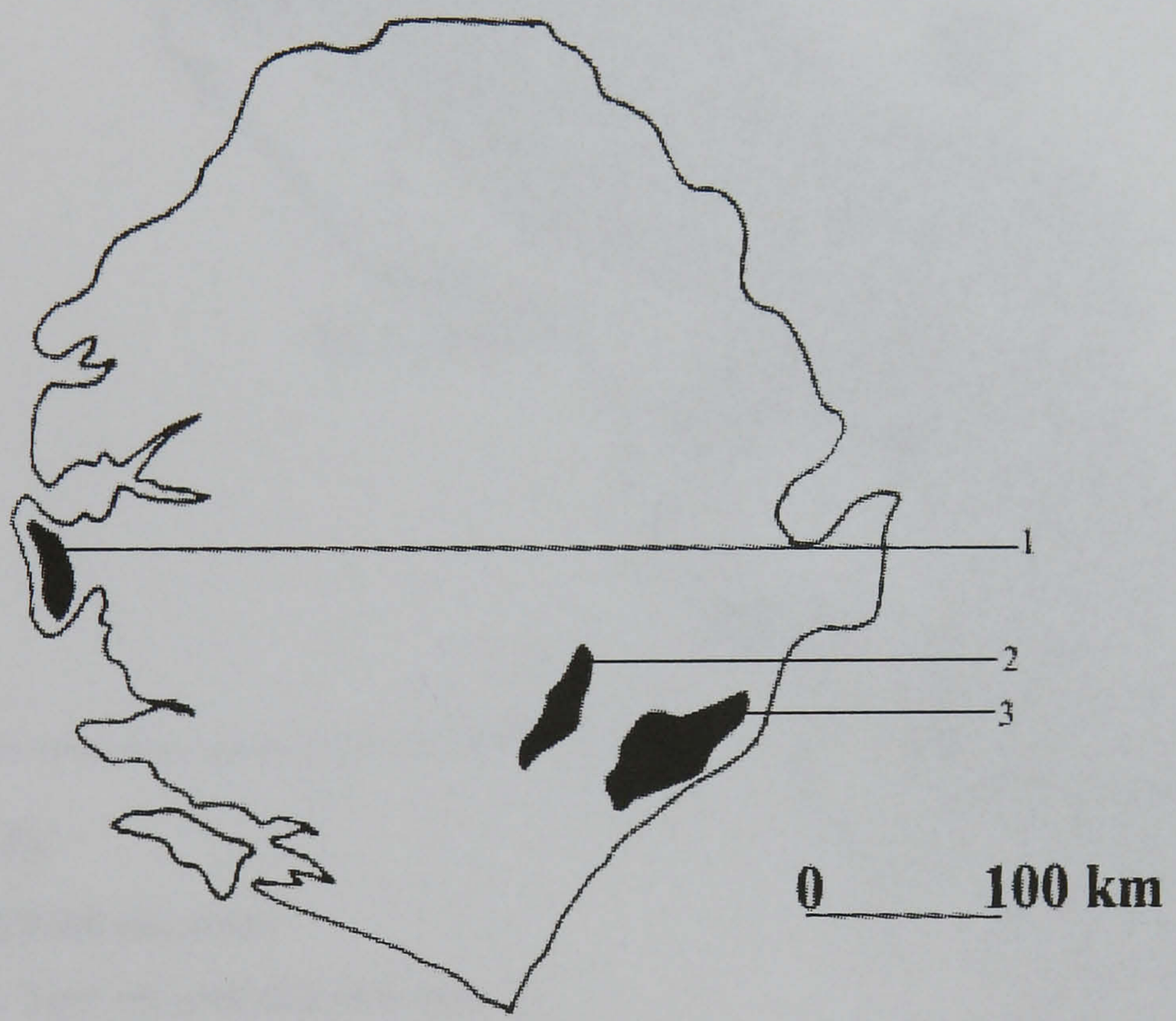


Fig 2.4. The Western Area Peninsula Forest Reserve and surrounding settlements

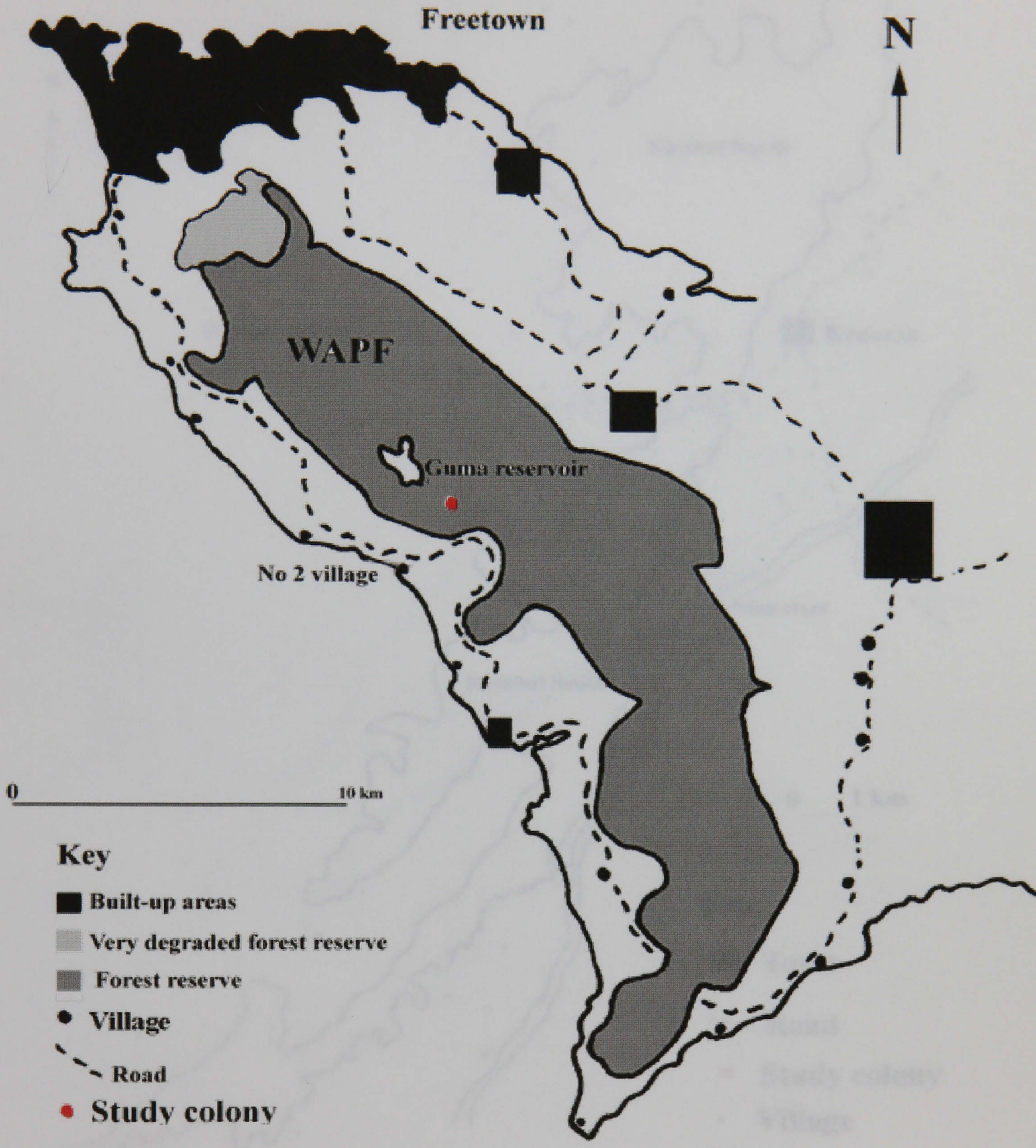


Fig 2.5.The Kambui Hills Forest Reserve and surrounding settlements

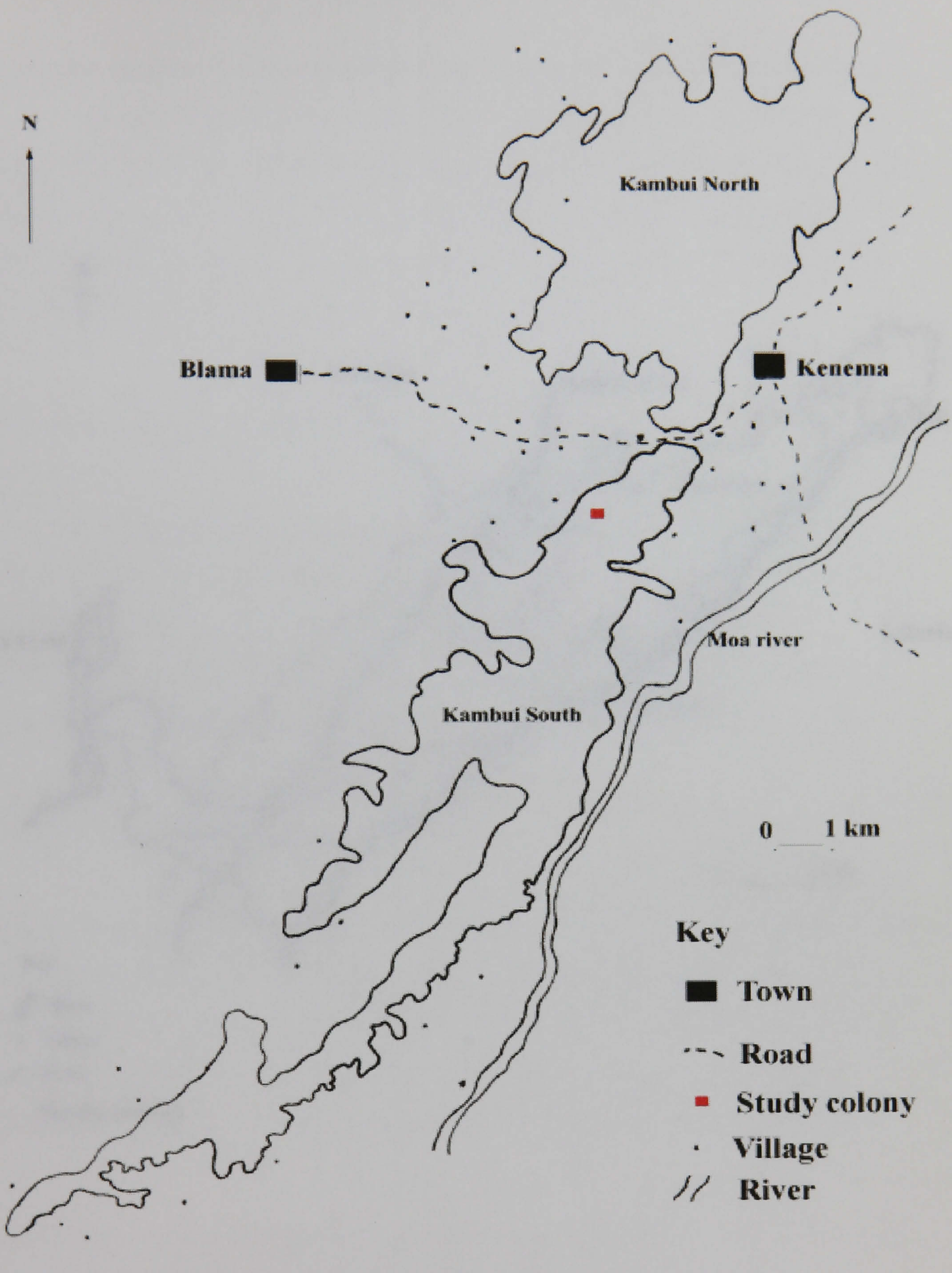
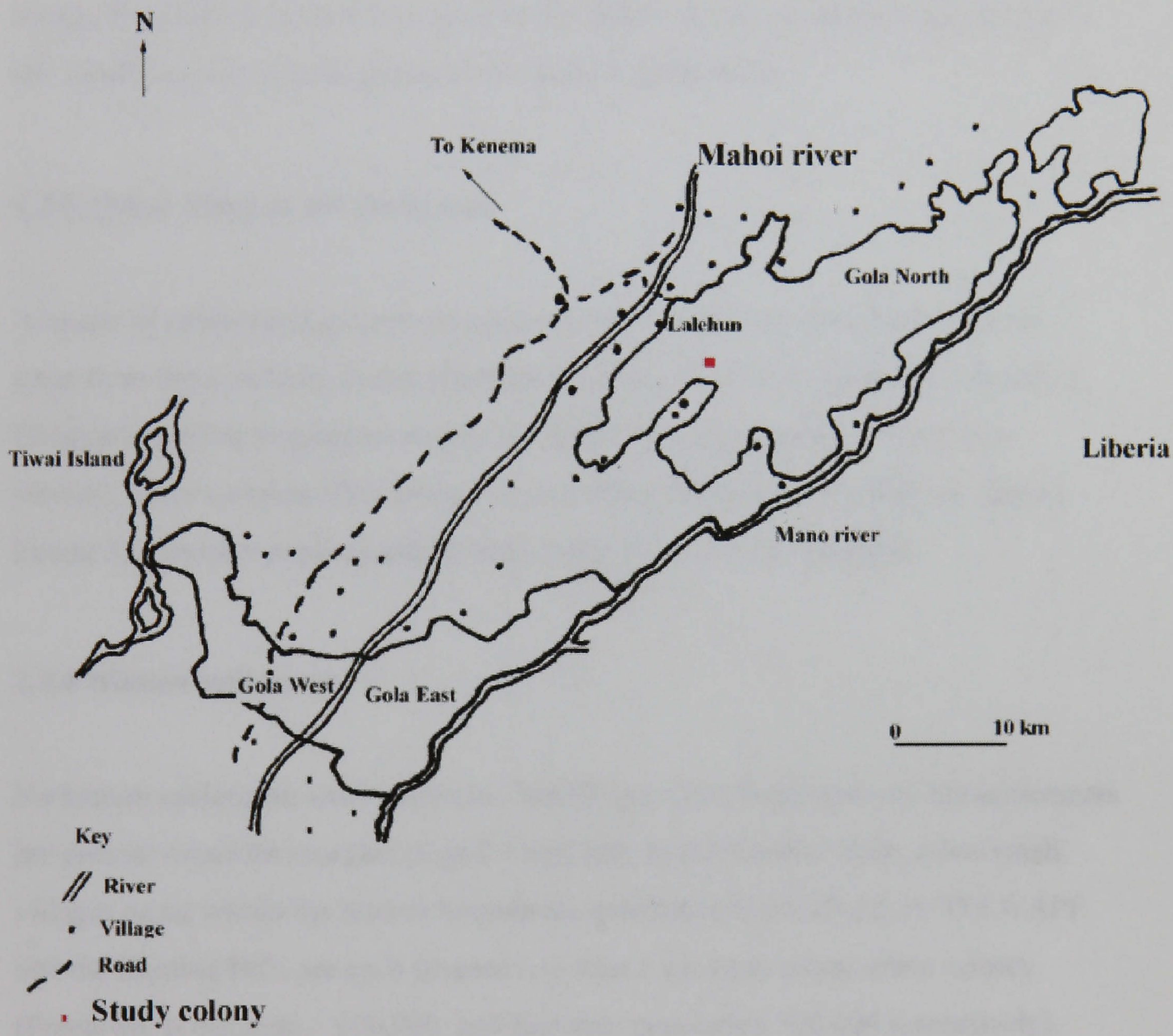


Fig 2.6. The Gola Forest Reserves and surrounding settlements



2.2.4. The avifauna of the study sites

Comparable numbers of bird species have been recorded in the WAPF and the Gola Forest ie 216 and 274 respectively (Field, 1974; Allport *et al*, 1989; Ausden and Wood 1991). All eleven of the forest-dependent threatened species that occur in Sierra Leone are known from the Gola forest and one globally threatened species (White-necked Picathartes) is known to occur in the WAPF.There are no previous records of any ornithological or biological surveys in the Kambui Hills.

2.2.5. Other fauna at the study sites

Animals of environmental concern present in the WAPF and Gola Forest reserves apart from birds include: Forest Elephant (*Loxodonta africana cyclotis*)(Gola only), Chimpanzee (*Pan troglodytes troglodytes*), Red Colobus monkey (*Procolobus badius*), Olive Colobus (*Procolobus verus*), Diana monkey (*Cercopithecus diana*), Leopard (*Panthera pardus*) and Jentink's duiker (*Cephalopus jentinki*).

2.2.6 Human influences

No human settlements exist within the WAPF and Gola forest reserves but settlements are present round the margins (Figs 2.4 and 2.6). In the Kambui Hills, a few small villages occur within the reserve boundaries in Kambui North (Fig 2.5). The WAPF and the Kambui Hills are each situated less than 5 km from major urban centres (Freetown: population > 600,000 and Kenema: population 300,000 respectively).

Parts of Gola Forest and the Kambui Hills have been logged in the past but no official logging concessions have ever been granted in the WAPF and there have been no large scale logging operations.

Iles *et al* (1993) estimated that 19% of Gola North and 42.5% of Gola East/West have been logged. Davies and Palmer (1991) cited the Kambui Hills as one of five forests in Sierra Leone where over-logging has occurred but gave no figures.

Apart from large-scale logging operations (which have been suspended in recent years due to poor security), human pressure on the reserves is mainly in the form of farming, hunting, tree-felling for timber and fuel-wood and to a small extent, clearing of land around the boundaries for settlements. The WAPF is most severely affected by hunting and tree-felling activities. Numerous footpaths form a network across the reserve and spent cartridges can be seen every few hundred metres (Thompson 1993). Primates are the main hunting targets (Davies & Birkenhager, 1990; pers. obs.). Illegal manual timber extraction operations have recently started at the northern and southern ends of the reserve (pers. obs.). In the Kambui Hills, chain-saw operations and illegal farming were the most frequently seen causes of encroachment. The integrity of the Gola forest has on the whole been well respected. Villages are concentrated to the west of the reserve (Fig 2.6) and this is where minor agricultural encroachment (invariably less than 2km into the reserve) has occurred.

2.2.7. Conservation status of the study sites

The Kambui Hills and the Gola Forest are both Forest Reserves. The WAPF is a non-hunting forest reserve which means that in addition to controlled land use, hunting requires a permit. However, enforcement of conservation regulations in all three reserves is minimal.

2.3. GENERAL METHODS

Details of the specific methods used in each section of the study are given at the start section concerned. Here, I describe procedures that were common to all sections of the study.

2.3.1. Field visits

The Kambui Hills and Gola forest are 320km and 400km respectively from Freetown where the author had teaching commitments. Field visits were therefore made to these sites once a month outside the breeding season (January - May; see chapter 4) and at least twice a month during the breeding season. Visits to the WAPF (only 5 km from Freetown) were more frequent and were carried out on an almost weekly basis, usually as day return trips. Site visits to the Kambui Hills and Gola forests averaged a week at a time. Site visits were made on a total of 508 days during the study.

2.3.2. Chronology and access

Preliminary studies started in the Gola forest and WAPF in 1990. Study colonies were located, field methods tested to assess their effect on *gymnocephalus* and reliable field assistants identified and trained (see Chapter 3). Intensive work was intended to start in 1991 and last for two to three years. These plans were disrupted by the outbreak of civil war in Sierra Leone in March 1991. Thereafter field work was conducted whenever security conditions permitted. Subsequently, work in the Gola Forest was abandoned in 1992. Field work was carried out in the Kambui Hills in 1992 and 1993 but this site was also abandoned at the end of 1993 because safe access was no longer possible. Field work was confined to the WAPF between 1994 and 1996, and largely restricted to brief visits for nest monitoring in 1994 and 1995.

Field assistants

Two field assistants (A.L. Macfoy and M. Musa) were employed and trained to monitor *P. gymnocephalus* nests in the Gola Forest area and the Kambui Hills in my absence (Chapter 3) and also to empty and store pitfall trap and malaise trap contents (Chapter 4) prior to analysis. One assistant was resident in each study area so that year- round monitoring was possible when security conditions permitted. In addition, information on the location of colonies in the Gola Forest and Kambui Hills areas was collected by A.L. Macfoy (Chapter 6) prior to ground-truthing by the author. Ali Koroma, a graduate student, organized logistics and participated in surveys of the distribution of *gymnocephalus* colonies throughout the country (Chapter 6). A. Okoni-Williams and S. Jusu helped to isolate fragments in faecal samples (Chapter 5).

Collaboration

A visit was made to Cameroon from 5th to 31st January 1996 to collect blood samples from the Grey-necked Picathartes *Picathartes oreas* for phylogenetic analysis (Chapter 7). The habitat and conservation status of *oreas* in Cameroon were also investigated (Chapter 6). R.C. Fotso, a Cameroonian ornithologist (See Chapter 6) provided transport and accomodation and guided me to *oreas* colonies. Sequencing of mitochondrial DNA from *oreas* and *gymnocephalus* blood samples was carried out by Dr. Ralph Tiedemann of the Institut fur Haustierkunde at the University of Kiel in Germany. The sequences were then sent to me for phylogenetic analysis at the University of Edinburgh (Chaper 7).

2.4. DATA ANALYSIS

All mean values are presented plus or minus one standard error. Normality of variable distribution was tested using graphical methods (eg normal probability plot) and the Kolmogorov-Smirnov test (Wilkinson, 1990). Means of normally distributed variables were compared using the Student's *t*-test or single factor analysis of variance.

Correlation relationships between such variables were evaluated by Pearson's (r) correlation coefficient (Sokal and Rohlf, 1995). Corresponding non-parametric tests (Mann-Whitney U test, Kruskal-Wallis one way ANOVA and Spearman's rank correlation coefficient) were used on nonnormal data and data with small sample sizes.

Simple transformations of variables (log, square root and arcsine) were used to reduce heteroscedastity and improve normality of data, where this was appropriate.

Association, independence or interaction between categorical variables were tested using chi-square procedures, Kendall's *tau-b* measure of association (the TABLES program in SYSTAT, Wilkinson 1990), or the log-likelihood ratio method (G-test; Sokal and Rohlf, 1995).

The effects of one or more independent factors on a single dependent factor were analyzed using single or multiple linear regression analysis on normally distributed variables. In the latter case, the "best" regression model was obtained by stepwise regression in a backward direction ie by first fitting all possibly important independent variables and then deleting those associated with t-values less than the critical value, starting with the lowest absolute t-value. A new multiple regression was fitted with the remaining independent variables and the process repeated until all t-values were greater than or equal to the critical value (MGLH program in SYSTAT, Wilkinson 1990).

Where multiple tests were used on the same data set to test the same null hypothesis, Bonferroni adjusted probabilities were used to determine rejection or acceptance of the null hypothesis.

CHAPTER THREE

BREEDING BIOLOGY AND BREEDING SUCCESS

3.1. AIMS

This chapter aims to describe the breeding biology of *Picathartes gymnocephalus*, for which previous information is lacking.

Two main questions are addressed:

1. What type of mating system do the birds use? How does this affect breeding success?
2. What are the levels of breeding success in *gymnocephalus* colonies? What factors contribute to these levels and what are the consequences of the mortality/survival rates for the population dynamics of the species?

Basic information on the biometrics of the species is provided as a background against which the breeding biology is described.

3.2. PREVIOUS WORK

Present information on the breeding biology of *Picathartes gymnocephalus* is scanty and derives largely from third-hand accounts (Sawyerr, 1965); brief, fragmentary observations (Glanville, 1954; Attenborough, 1955; McArdle, 1958; Grimes, 1963; H. Mudd and R. Martins, pers com); and from captive birds (Dekker 1971, 1973; Faust 1970; McKelvey 1981; Collar and Stuart 1985). An exception is a study in which detailed breeding records were kept for a period of three years between 1963 and 1966 at one site in Ghana (Grimes, 1964; Grimes and Darku 1968). However, observations were mainly directed toward determining the timing of breeding and these authors gave little information on other aspects of the breeding biology.

There has been more systematic study of *Picathartes oreas*. Early descriptions were also qualitative and fragmentary (Webb, 1949; Durrell, 1949; Serle, 1952b; Kieffer, 1953; Brosset 1965a, 1965b; Golding, 1968; Moore, 1974; Brosset and Erard, 1986) but Tye (1987) carried out a quantitative investigation of the incubation and nestling stages of adult *oreas* at three nests in montane habitat in southwest Cameroon and Fotso (1993) provided empirical information on breeding season and nestling growth in lowland southern Cameroon, though only at a single nest. These are the most complete studies of *Picathartes* to date but their significance is constrained by small sample sizes and the fact that none of the birds in either study was individually identifiable. This chapter presents a quantitative description of the reproductive biology of *gymnocephalus* using colour-ringed birds where possible.

3.3. STUDY COLONIES

Study colonies were located in the WAPF, Kambui Hills and Gola Forest (Figs 2.4, 2.5 & 2.6: Chapter 2).

In the WAPF, the study colony comprised three nests on a rock (7.4m x 16.1m) at the confluence (30° slope; 90m asl) of two tributaries of the No.2 river. The colony was accessible via a nature trail for tourists which ran west to east from the main Peninsula Road in the vicinity of No.2 Village (Fig 2.4), through farmbush and secondary forest into mature high forest above the 100m contour.

The study colony in the Kambui Hills comprised seven nests on the vertical southwestern face of a rock, 5.5 m high and 15.4 m wide, located on the western side of the Kambui Hills range, midway along its north-south axis (Fig 2.5). It was situated on the sandy bank of a 2m-wide stream on the plateau of a ridge about 2 km from the reserve boundary. Although the colony was completely surrounded by mature closed canopy forest, sizeable patches of forest regrowth caused by illegal farming occurred to the west (50m away), north-east (250m away) and southwest (1 km away). Chain-saw operators were active 2-4 km from the study colony.

The Gola Forest study colony was located in the south-west corner of the Gola North Forest Reserve (Fig 2.6). The colony comprised six nests; three on a vertical face of a rock - 13.5m x 13.5 m - and three on a horizontal overhang formed by a fissure across the rock face. The rock was situated on a 65° slope of a narrow valley, about 25m from a seasonally flowing stream. The surrounding vegetation was mature closed canopy forest of the *Heriteria/Lophira* complex (See Chapter 2). Access was via an old logging road from the town of Lalehun (Fig 2.6).

3.4. METHODS

3.4.1. Observations at nesting colonies

A total of 508 hours was spent observing birds at different stages of the breeding cycle in the WAPF (206 hrs), Kambui Hills (254 hrs) and the Gola forest (48 hrs). Total observation time was distributed between different stages of the breeding cycle as follows: non-breeding season - 197 hours; incubation - 218 hours and nestling stage - 220 hours (the sum of observation times for different stages of the breeding cycle is greater than the total observation time because nests at different stages of the breeding cycle were sometimes observed simultaneously).

Birds were observed with 8 x 30 binoculars from a hide (1.5m x 1m x 1m), about 10m from each study colony. Each hide was made from leaves and branches but the side facing the colony was reinforced with dull-coloured rice sacking. Observations were recorded in a field notebook during each observation session and/or dictated into a hand-held tape-recorder, especially during rain.

Two methods - the individual focal sample method and simultaneous scanning - were used to record bird behaviour (Altmann, 1974). Both methods were supplemented by opportunistic observations.

In the individual focal method, the behaviour of a single individual (sometimes marked) was observed for a fixed period of time (Altmann 1974). In addition, a particular nest in the colony was designated the focal unit and the behaviours of all birds seen to be associated with that nest (sitting in, guarding etc) were recorded over fixed time periods. The birds associated with each nest were few, the intervals between changes in behaviour relatively long and birds leaving the nest could be kept in view until they left the colony area. It was therefore possible to record behaviour at more than one "focal nest" at the same time.

Scanning was most useful immediately prior to the start of egg-laying when several birds (2- 12) congregated at the breeding colonies at about the same time each day and carried out various activities, in a well-defined area in front of the breeding rock (Section 3.5.2). The birds were scanned at fixed time intervals and the behaviour of each individual recorded.

Parental behaviour was quantified by recording the number and duration of the following activities :

a) Incubation/brooding stints: the time spent sitting on eggs or brooding nestlings without interruption. An interruption was arbitrarily defined as a time interval of more than 30 seconds spent away from the nest contents;

b) incubation/brooding bouts: the total continuous time each bird spent on parental duty at a nest before being replaced. A bout could consist of several stints;

c) trips to feed nestlings;

d) nest building trips/behaviour;

e) aggressive encounters - an actual fight, or one bird chasing another without any immediate subsequent behaviour to indicate that the chase might be part of some other type of interaction;

f) nest visits - a bird sitting in a nest or perched on its rim for less than one minute without incubating eggs or feeding nestlings;

g) preening;

h) hopping about;

i) standing still (for more than one minute);

j) perched on a branch;

k) bathing and

l)foraging for food.

Active behaviours were given precedence over passive ones whenever two or more categories occurred simultaneously.

3.4.2. Nest inspections

Nests were inspected daily during field visits and the nest contents recorded. Usually, between 10 and 15 days of inspections were carried out per month during the breeding season and three to five inspections outside the breeding season. The area beneath nests was carefully searched for evidence of the potential causes of any mortality which may have occurred between visits (eg. animal fur or any other body parts). Field assistants checked nests at least once every fortnight throughout the year, in my absence.

Nests which were out of reach were inspected by means of a mirror at the end of a long pole or by using a ladder fashioned from fallen branches at the site. This was carefully hidden away at the end of each visit.

The procedures for inspecting and handling nests contents were tested during a feasibility study carried out in the WAPF and Gola forest in 1990, before it was decided to continue with the study. Two colonies each, in the WAPF (three and four nests each) and Gola forest (six and five nests respectively), were observed for 93 hours (WAPF-78 hours; Gola-15 hours). Eleven eggs and 12 nestlings were handled at the 18 nests and the reactions of adults monitored closely. Handling was only carried out when birds were not sitting in the nest. Birds did not give alarm calls when nests were approached but moved away and watched operations at the nest, while occasionally carrying out minor maintenance activities such as preening. In all cases (n = 13 occasions) birds returned to the nest shortly after I left and did not show any noticeable deviation from their usual behaviour. However, a 199g nestling left the nest soon after being weighed, measured, ringed and blood extracted from a wing vein (see

Chapter 7). Consequently, during the rest of the study, nestlings were only ringed and blood extraction procedures carried out (which necessitated extra handling time) when less than 150g in weight. This reduced the risk of nestlings leaving the nest prematurely as a result of handling.

3.4.3. Trapping, ringing and measuring birds.

Adult birds were trapped in order to record body measurements and weights, determine their state of moult, to fit colour-rings to identify birds individually and to collect blood samples (Chapter 7).

Birds were trapped either by taking them from the nest at night or by mist-netting. Roosting adults slept with their heads tucked down into the nest and usually facing the nesting rock. Nesting sites were approached quietly after 21.00 hours, and a powerful torch shone into a nest to dazzle the occupant, which was then taken from the nest. This method was discontinued after a bird struggled vigorously on capture.

Birds were mist-netted by setting up four 18m nets, 100-200m from nesting colonies, on the relatively fixed routes which the birds used for going to and from their nesting sites. Nets were opened for about four hours each day, on two successive days in not more than two weeks of any particular month in which trapping was undertaken. This minimised disturbance at any particular colony and reduced the possibility of birds becoming trap-shy.

Birds which struggled vigorously on being handled, were released immediately. The bare head bruised easily and care was taken to avoid this. Covering the eyes during handling, as in many other species, calmed birds during examination. Trapping was suspended as soon as egg-laying started at any particular colony. These precautionary procedures account for missing records in some datasets (eg Appendix 3.1).

Each bird trapped was fitted with two to four colour rings in a unique arrangement which allowed individual identification.

Trapped birds were weighed, their bill, wing, tarsus and tail lengths measured; and the state of moult of the remiges and rectrices recorded before release (Chapter 4). Birds trapped during the day were released about 30 - 60 minutes later at the site of capture. Birds trapped at night were kept in bamboo cages overnight and released at dawn to reduce the risk of their being taken by predators at night after release.

Eggs and nestlings were weighed and measured daily during the twice-monthly field trips. Eggs were marked with numbers, using a soft felt-tipped pen, to indicate nest location, and the laying sequence within a clutch when this was known. Egg dimensions (maximum width and length) were taken with dial vernier calipers correct to 0.1mm.

Nestlings were initially marked with spots of nail varnish to distinguish between siblings, then colour-ringed when 14 - 21 days old or over 100g in weight.

All weights were taken with a Pesola spring balance which was checked for accuracy and re-calibrated, if necessary, after each trapping trip.

The flattened wing-length of adults and nestlings was measured with a stopped wing rule, as was adult tail length. The wing chord was measured from the carpal joint to the longest primary, or to the distal end of the phalanges in nestlings in which the primaries had not yet erupted. Tail length was measured from base to tip of the longest (central) feather.

Bill length and tarsus length were taken with dial vernier calipers correct to 0.1mm. Bill length was measured from the tip to the union of the bill with the skull, which was demarcated by the margin of the yellow skin on the head. The tarsus was measured from the pit at the junction of the tibiotarsus and tarsometatarsus to the last complete scale before the toes diverge.

Primary and secondary moult were scored when birds were examined (see Chapter 4).

3.4.4. Examination of museum specimens

The body measurements of *gymnocephalus* and *oreas* specimens at the British Natural History Museum at Tring, were recorded in a similar manner as described above.

3.4.5. Analysis of breeding success data

Nestling and egg survival rates were estimated using Mayfield's method (1961, 1975; Johnson, 1979; Hensler and Nicholls, 1981; see also Ashkenazi & Yom-Tov, 1997) which considers survival on a daily basis.

The daily mortality rates (*m*) for any period were obtained by dividing the total number of losses by the total exposure; where exposure was taken as the product of the number of nestlings or eggs in the sample and the amount of time each was under observation. The corresponding daily survival rate *dsr* was 1 - *m*. The average survival rate (*asr*) for the incubation (*i*) and nestling (*n*) periods were obtained by raising the daily survival estimator for each period to the power of its duration ie $asr = dsr^i$ or dsr^n. Average nesting success values (probability that an egg will survive from laying to fledging) were obtained from the product of the probabilities for the separate stages.

The standard error (s.e.) of Mayfield's daily survival estimator was calculated using the method given by Johnson (1979) where s.e. is the square root of the variance of the daily survival rate (*dsr*) and this variance is the inverse of $(\text{exposure})^3/(\text{exposure-losses}) \times \text{losses}$. Approximate 95% confidence limits for *dsr* are: *dsr - 2 s.e* to *dsr + 2 s.e*. Lower and upper confidence limits for asr^t ie average survival rate for a period of *t* days is obtained by raising the corresponding confidence limits of *dsr* to the power *t*.

Estimates of survival rates were compared using Johnson's (1979) method where the ratio of the difference between two estimates to its standard error is taken as a normal variate with zero mean and unit variance (the variance of the difference equals the sum of variances of the two estimates). Deviations from unity indicate the probability

with which survival rates differ between categories.

Nests seen only once were not included in the analysis of breeding success because they did not span any period of time. A nest lost during an interval of several days was arbitrarily assumed to have been lost on the day at the middle of the interval (Mayfield, 1975). This is reasonable for intervals between visits averaging up to about 15 days (Johnson, 1979).

3.5. RESULTS

3.5.1. Biometrics

Biometric data were recorded from 31 adult-plumaged *gymnocephalus* in the field (Appendix. 3.1.) but six retraps were excluded from the dataset in order to maintain independence of data points. Data were obtained from every month of the year except October and December

Body weights

The mean body weight of adults was 219.6g±3.38g (n = 24)(Appendix 3.1). Weights recorded at the same study site (Kambui Hills) between July 1992 and May 1993 did not show any clear seasonal variation pattern, perhaps because of the small sample sizes (Fig 3.1a.). An individual (*w o w*; *y*) first captured in March and retrapped 51 days later in May had lost 10.1% of its initial weight (Fig 3.1a. & Appendix 3.1) suggesting that perhaps the end of the dry season (April-May) was not a favourable period. The weight of another individual (*w g w*; *y*) remained almost constant during the same period. Three birds retrapped over longer periods (193, 213 and 275 days respectively) showed minimal weight loss (< 2%; n = 2) or had gained weight (3.5%; n = 1; Appendix 3.1).

Body measurements

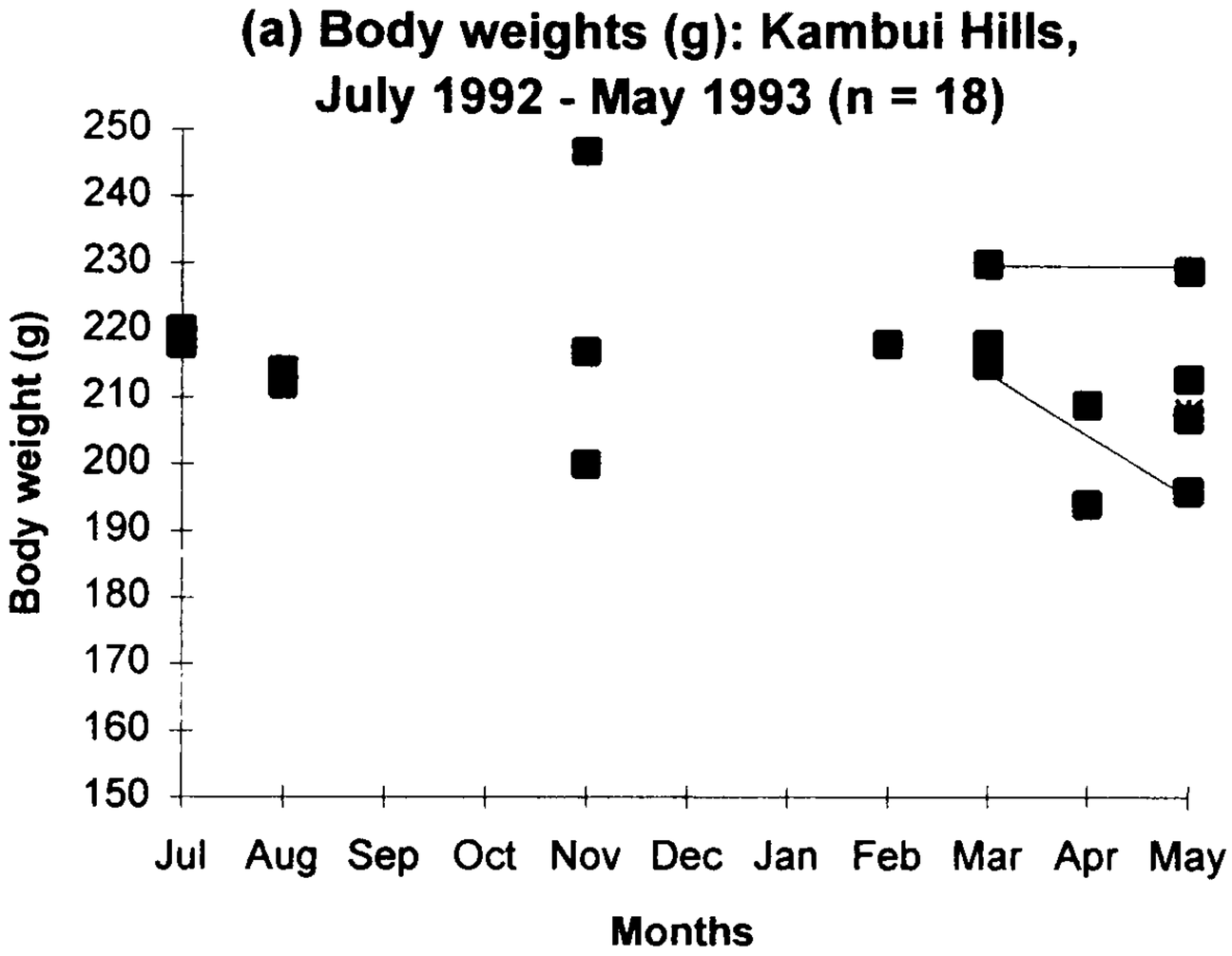
The wing lengths of unsexed adults ranged from 152-176mm with a mean of 163.8±1.83mm (n = 24; Table 3.1). Mean bill length was 33.1±0.32mm and ranged from 30-35mm while tarsus length ranged from 50-75mm with a mean of 63.8±1.63mm (n = 21 in both cases, Table 3.1). Mean adult tail length was 182.8±1.77mm (range = 170-205mm, n =21; Table 3.1).

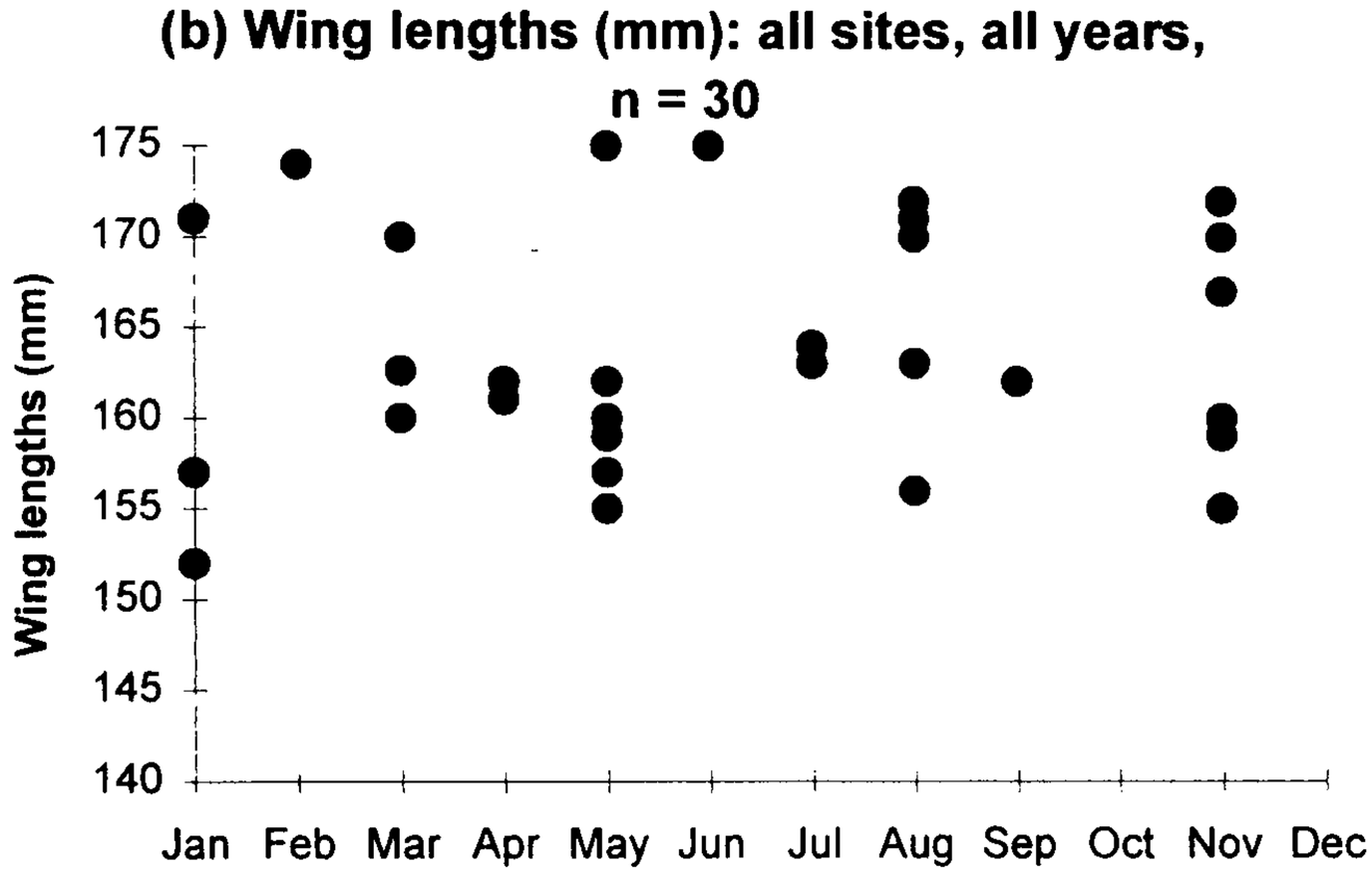
Wing and tail length measurements did not show any systematic variation during the study (Figs 3.1b & c). This may indicate that adult *P. gymnocephalus* did not show any systematic shortening of the wings and tail as a consequence of moult and/or abrasion during the year. However, asynchrony of moult may obscure any such effects in a population and data from retrapped adults showed that there were marked changes in wing lengths in some individuals during the year (Appendix 3.1).

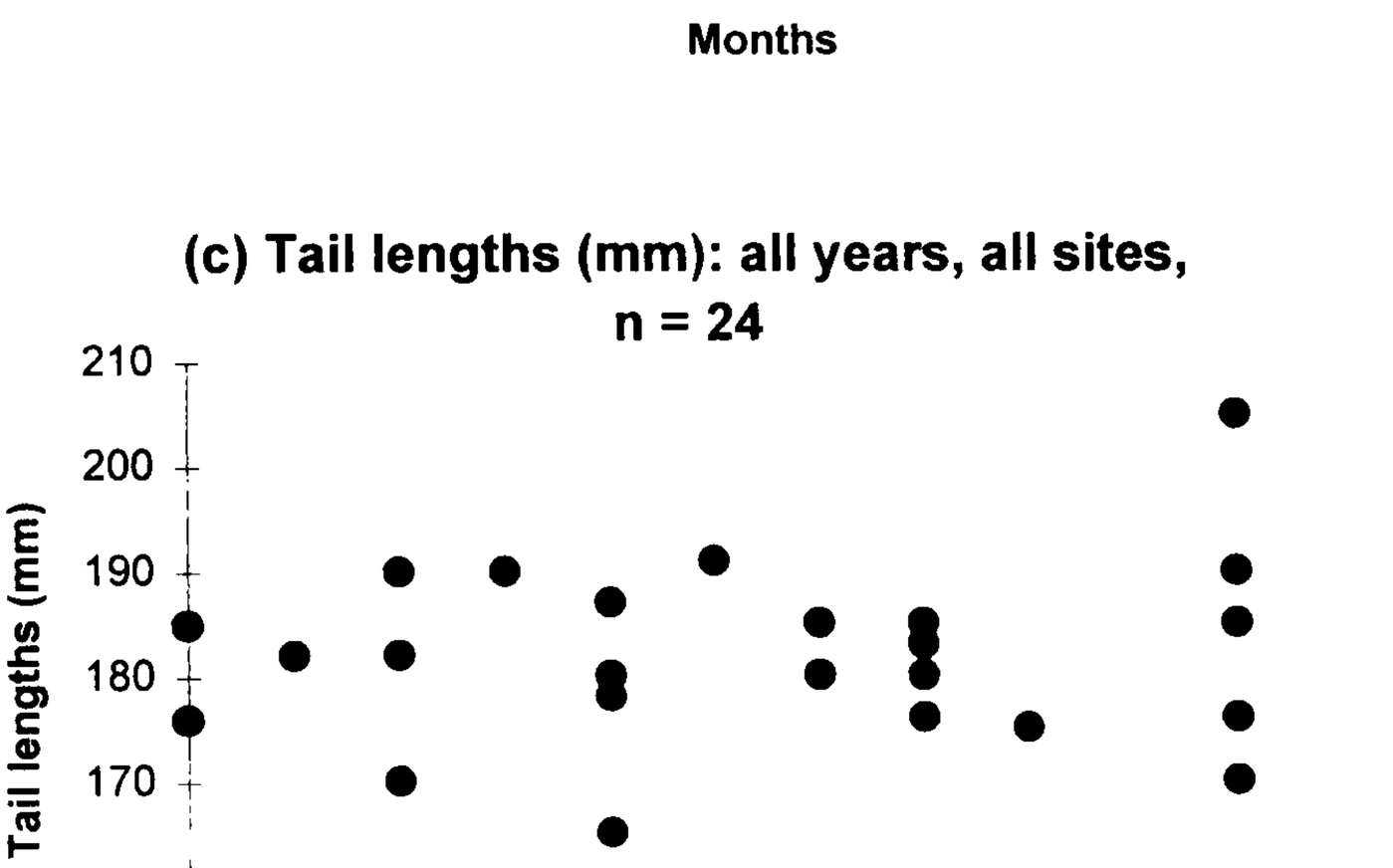
Table 3.1. Mean body measurements(mm) ±s.e. (n) of adult *Picathartes* taken in the field and from museum specimens. All *oreas* measurements were taken from museum specimens. Museum specimens of *gymnocephalus* were all female; individuals measured in the field were unsexed

	Body measurements (mm):			
	Wing	Bill	Tarsus	Tail
P. gymnocephalus				
Field	163.8±1.8(24)	33.1±0.3(21)	63.8±1.6(21)	182.8±1.8(21)
Museum	159.6±2.0(7)	32.4±0.68(7)	50.5±0.94(7)	193.5±2.0(7)
P. oreas				
Males	158.3±2.53(6)	37.0±0.65(6)	49.4±0.94(6)	155.2±3.35(6)
Females	155.6±2.72(5)	35.4±1.14(6)	46.2±0.78(6)	152.0±3.04(5)
Both sexes	156.7±1.8(11)	36.2±0.7(12)	47.8±0.8(12)	154±2.7(11)

Fig 3.1. Body weights (g) and measurements (mm) of adult *Picathartes gymnocephalus* trapped at different times of the year. Lines join weights of birds trapped more than once in the same year.







Sexual dimorphism

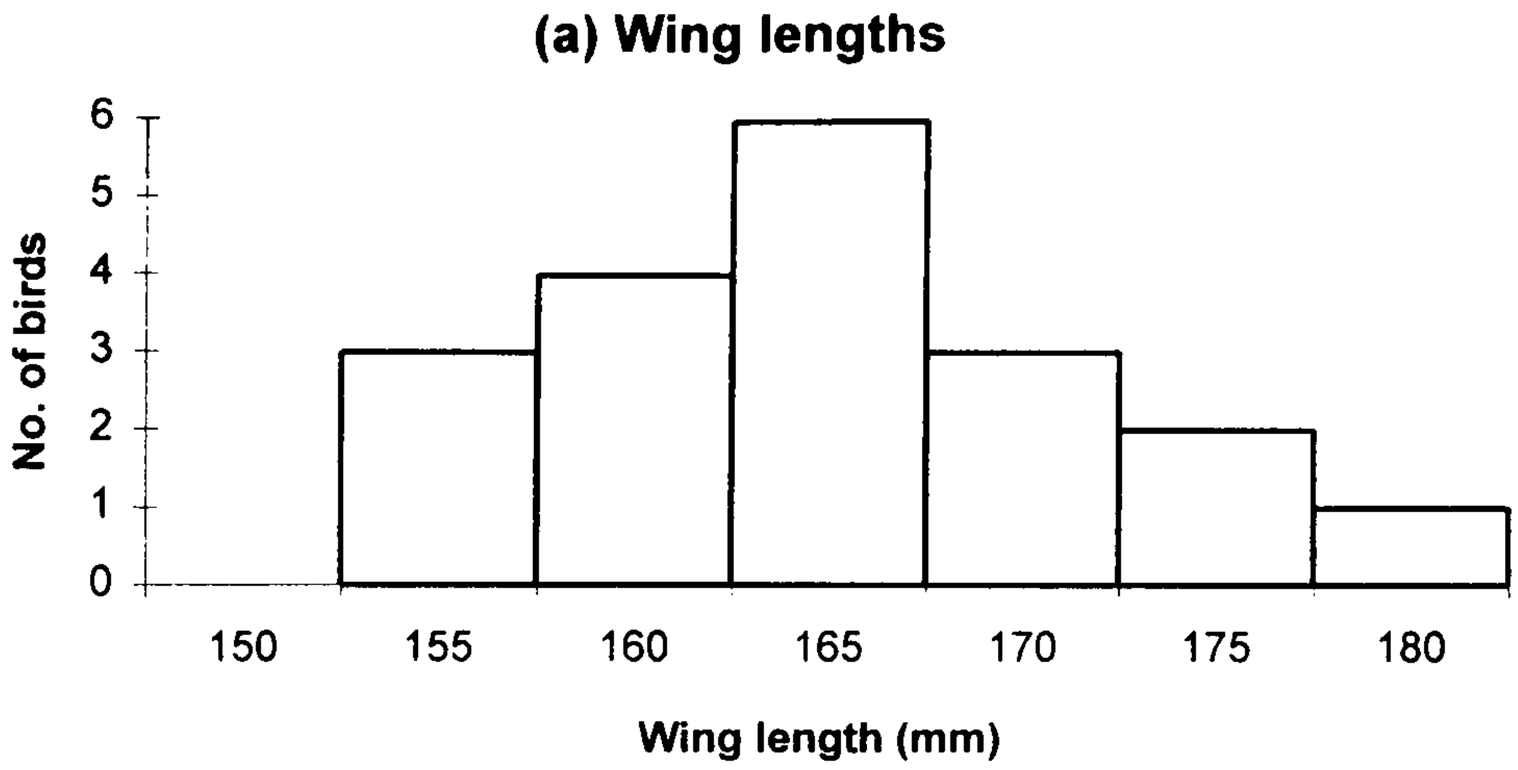
Picathartes is sexually monomorphic. Observable or measurable sexual differences should prove useful in future research and/or conservation management of the species, so an effort was made to detect such differences.

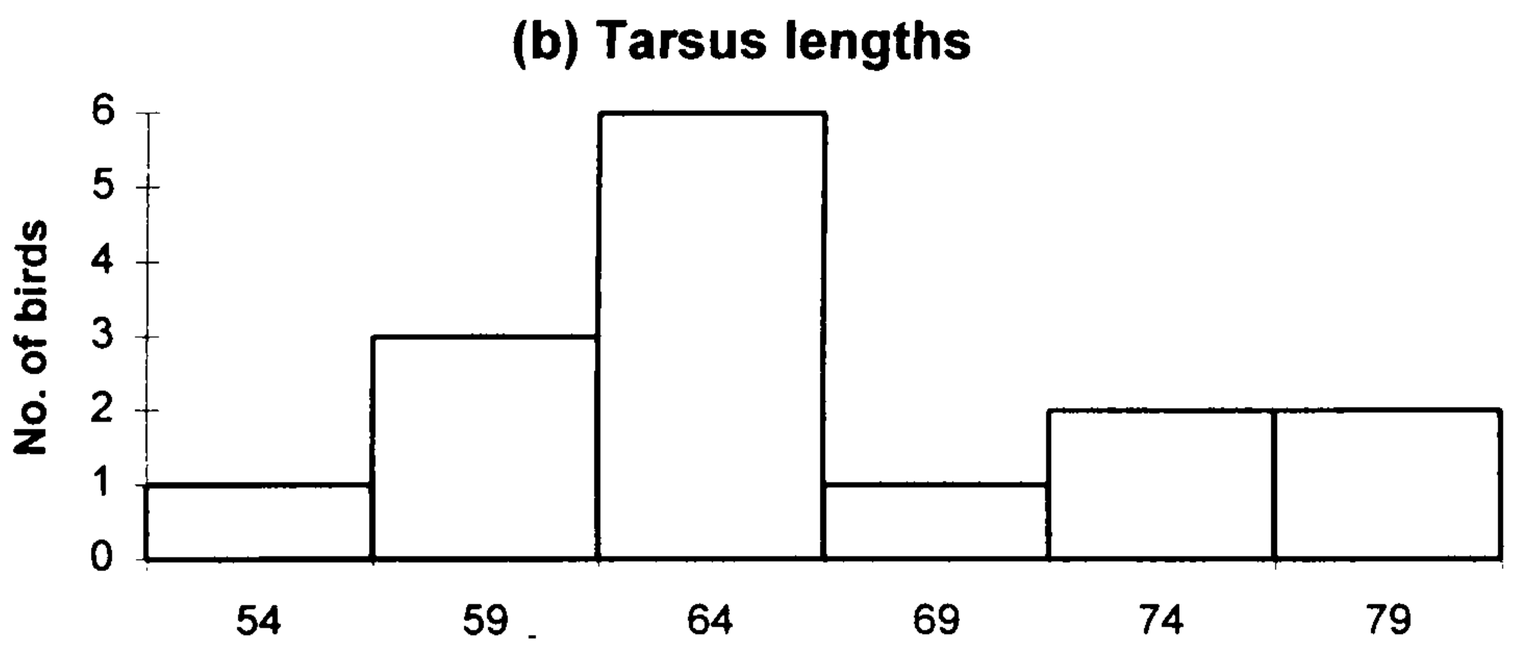
There were no observable differences in plumage, eye-colour (pupil: blue-black; iris: brown) or leg colour (bluish-grey) between individuals examined in the field (n = 25). No brood patches were found on any captured birds.

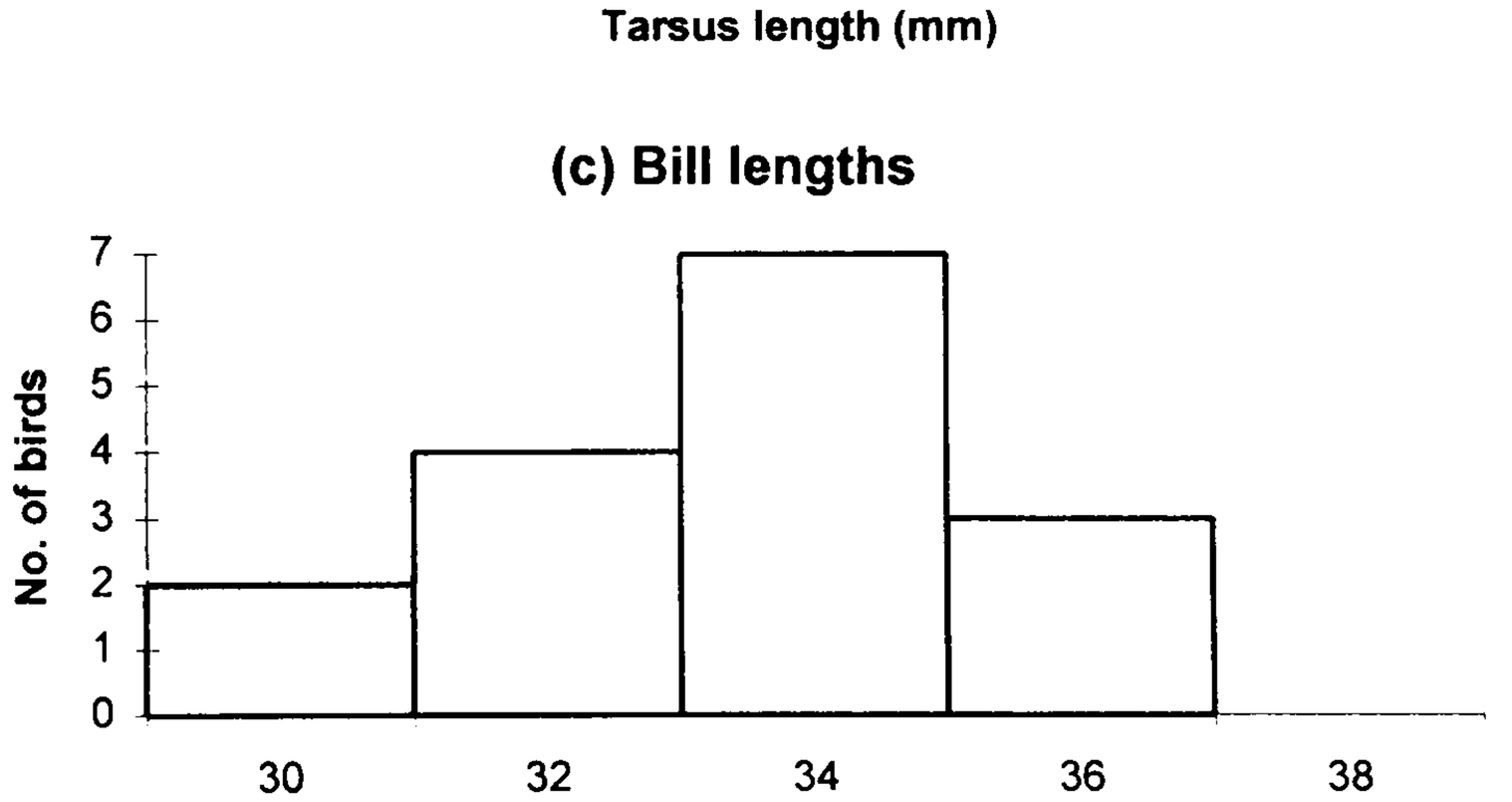
Body measurements did not deviate from a normal distribution (Fig 3.2: Kolmogorov-Smirnov one sample tests: P = 0.217; 0.581; 0.149 and 0.099 for bill, tail, tarsus and wing lengths respectively). However, given small sample sizes, such as those obtained here, two closely similar overlapping normal distributions due to slight differences in the sizes of the two sexes would appear as a single distribution. Also the sex ratio of the trapped sample could have been significantly skewed toward one or other sex, in which case the body measurement distributions would appear normal.

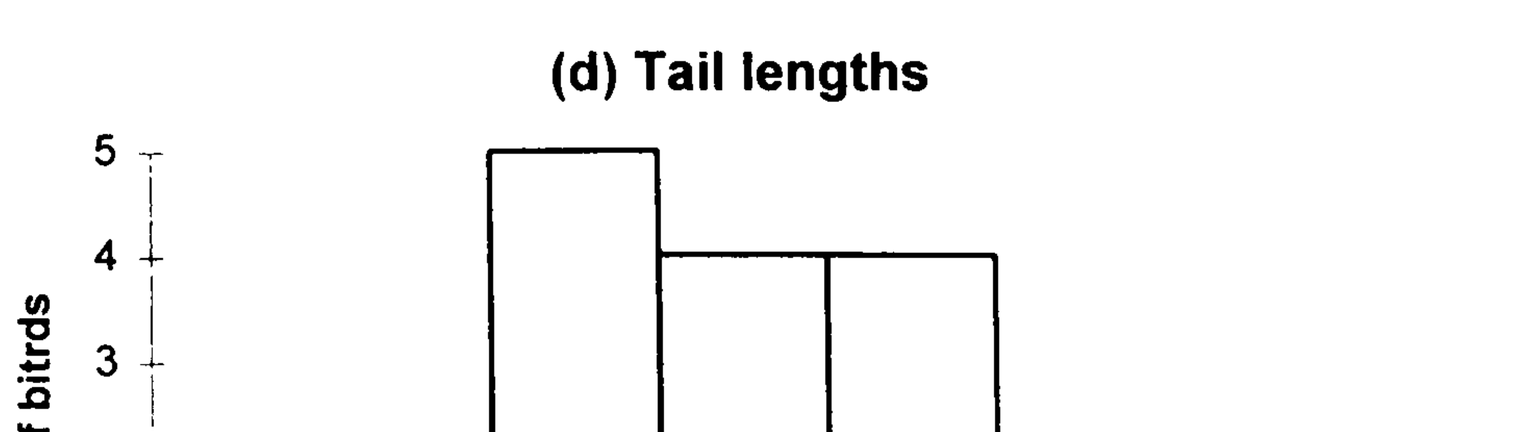
In order to investigate the possibility of sexual dimorphism in size further, male and female body measurements of museum specimens of *Picathartes* were compared. All sexed *P. gymnocephalus* specimens at the Tring Museum were female, so this comparison was only possible for *oreas*. Body measurements were greater in males (n=6) than females (n=6; Table 3.1.), with the difference in tarsal measurements between the sexes being statistically significant (Table 3.1.& Appendix 3.2; $t = 2.62$, $p < 0.03$, $df = 10$). These results suggest *oreas* males are larger than females and this difference is detectable by taking tarsal measurements. The 95% confidence limits for male and female *oreas* tarsal measurements were 51.82 - 47.0 mm and 48.21 - 44.19 mm respectively; so a useful rule of thumb in the field would be that birds with tarsal measurements greater than 48mm are males.

Fig 3.2. Frequency distributions of body measurements (mm) of adult *Picathartes gymnocephalus*









Species differences in body size

As a matter of biological interest and in order to provide background information for interpreting any differences in ecology and behaviour between the two species which the study might reveal, I compared the body measurements of museum specimens of *gymnocephalus* and *oreas* (Table 3.1 & Appendix 3.2).

The mean tail, tarsus and wing lengths of *gymnocephalus* were greater than those for *oreas* with the differences in tail length ($t = 12.6$; $df = 16$) and tarsus length ($t = 2.258$; $df = 13$) being statistically significant (t-test: $p < 0.001$ and 0.05 respectively). But, *oreas* bill lengths were significantly greater than those of *gymnocephalus* ($t = 3.992$; $p < 0.002$, $df = 15$; Table 3.1).

Measurements from museum skins are usually shorter than those from live birds due to shrinkage. Shrinkage may vary between species and with preparation technique (Jenni and Winkler, 1989). These factors need to be taken into account if these results are to be applied to natural populations. Field measurements of *gymnocephalus* tarsus ($t = -7.04$; $df = 26$) and wing ($t = -2.2$; df 13) were significantly greater than measurements of museum specimens (t test: $p < 0.001$; $p = 0.02$) but field and museum measurements of bill length did not differ significantly (Table 3.1; $t = -0.979$, $df = 9$, $p > 0.2$). Although field data for *oreas* were not available for direct comparison of the shrinkage factor in the two species, these results make it likely that the differences in size observed between museum specimens of the two species, also occur in natural populations ie *gymnocephalus* is larger in size than *oreas* but *oreas* has a larger bill.

3.5.2 Pre-breeding behaviour

In April and May, birds were seen at the Kambui Hills nesting site, only in the mornings and evenings (08.00 - 10.00 and 16.00 - 19.00 hours)(Fig 3.3). Numbers seen per day ranged from 2 to 9 and total time spent at the site was 12.2% of

observation time (n = 30 hours over 3 days with observations from 08.00-18.00 hours). Birds arrived at the site singly or in pairs, from the same general direction every day, and carried out maintenance activity such as bathing and preening. Occasionally, brief visits were made to nests and interaction between individuals occurred as short chases and displacement at nests.

The duration and frequency of site visits increased as the breeding season approached. In July (eight and four weeks prior to the start of egg-laying in the Kambui Hills and WAPF respectively), birds visited the breeding sites at intervals throughout the day (Fig 3.3). The average time spent at the site on each visit was 31.1±17.8 mins in the Kambui Hills and 25.0±19.8 mins in the WAPF (n = 9 and 19 visits respectively).

Fig 3.4 shows a time budget of adult *P. gymnocephalus* behaviour at nesting sites in the Kambui Hills and WAPF four to eight weeks prior to egg-laying. The total time birds spent at both nesting sites was 22% of observation time (56.5 hours over 7 days with observation from 08.00 - 18.00 hours). More than half of this time was spent repairing damaged nests (31%), perching on nest cup rims (17%) and sitting in nests for brief (5-60s) periods (14.2%; Fig 3.4).

Two individuals co-operated in repairing each nest (resealing holes in the bottom of nest cups and heightening nest cup walls). As in most passerines, one bird remained at the nest and arranged nesting material (mainly wet mud but also dried leaves, fibres and twigs) brought by the other. Roles were frequently switched and birds occasionally swallowed and regurgitated mud before using it on the nest.

Apart from nest repair and nest visits, most of the remaining time at breeding sites was spent autopreening(8.8%, allopreening was seen only once), hopping about without being engaged in any other observable activity (14.2%)(this sometimes developed into short chases between pairs) and simply standing still (>60s)(4.8%).

Other activities (9.9%) included bathing, foraging, chases and fights, and a peculiar group behaviour pattern seen only in the Kambui Hills; once during the structured

Fig 3.3. Time spent by adult *P. gymnocephalus* at nesting sites in the Kambui Hills and WAPF prior to egg-laying

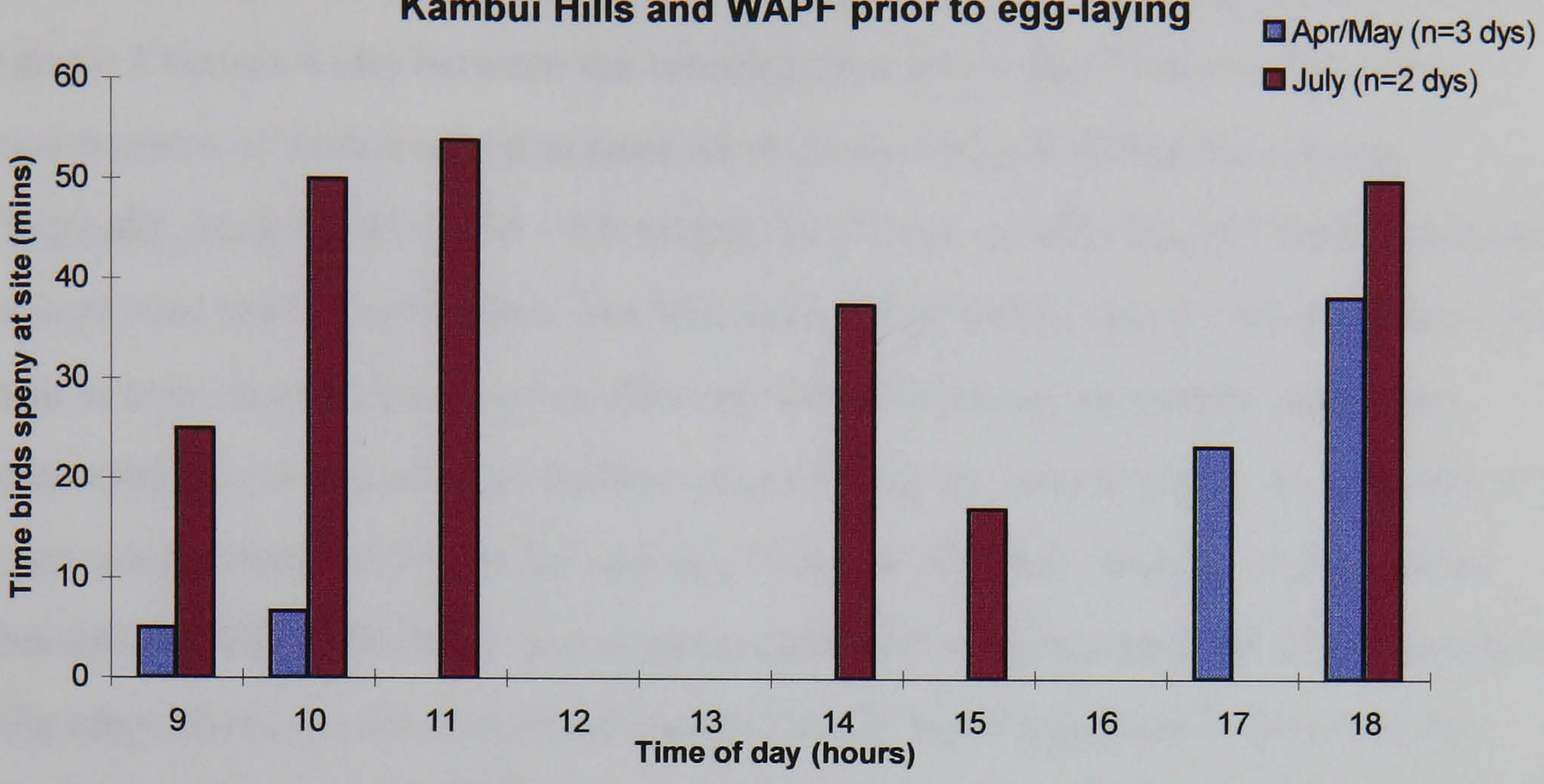
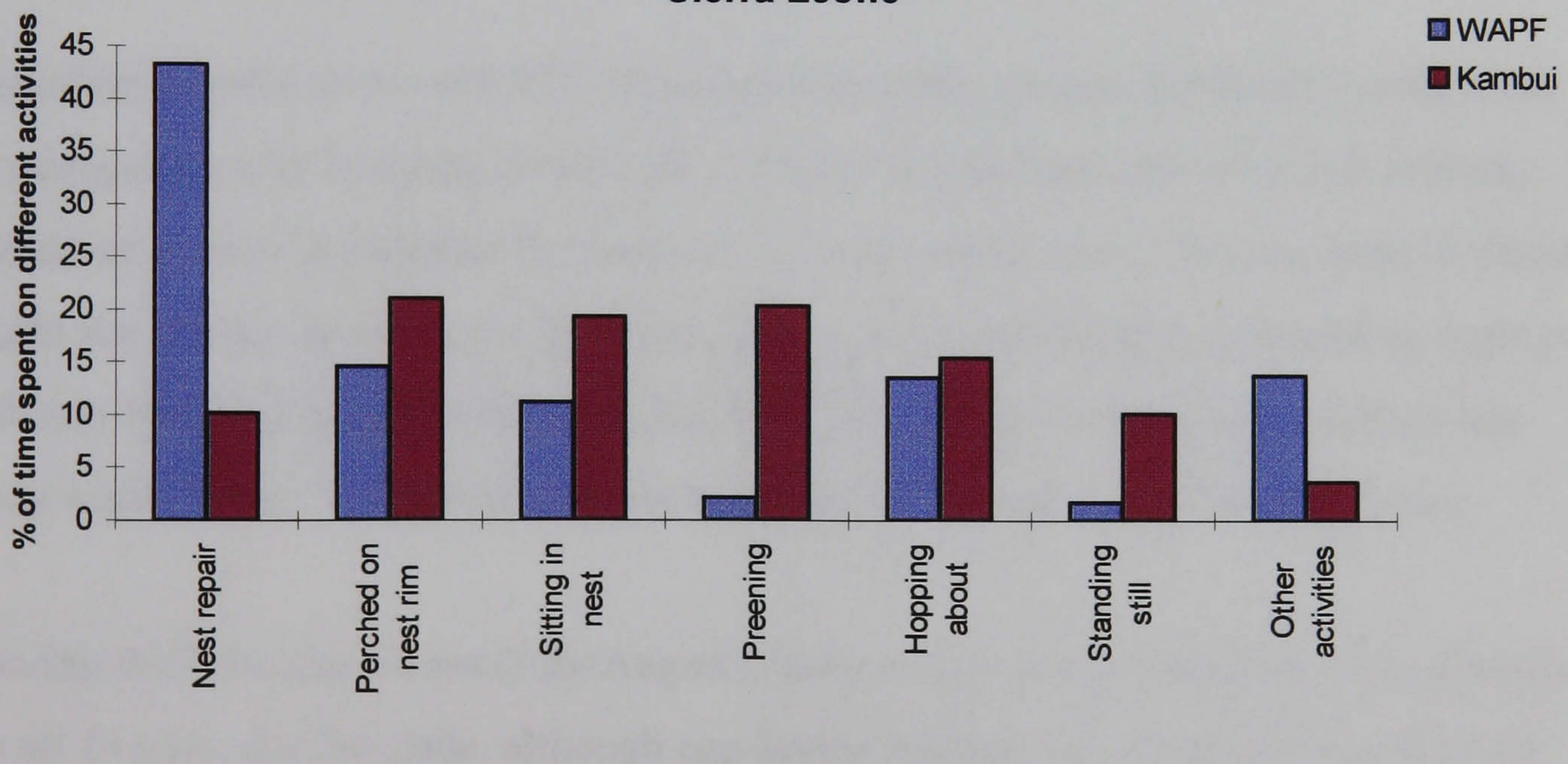


Fig 3.4.The proportion of time spent by *P. gymnocephalus* on different activities, 4-8 weeks prior to egg-laying at two nesting sites in Sierra Leone



monitoring sessions in July and twice more during opportunistic observations in August. On each occasion, the behaviour was observed between 18.00 and 19.30 hours; 6-7 birds were involved and the activity took place on a small strip of sand (about 2 metres wide) between the breeding rock and a small stream. The main components of each interaction were short chases and a brief bowing display. Typically, birds standing 0.5 - 1.0 m apart in a loose, poorly-defined circle made short abrupt runs toward each other. The bird approached would move a short distance off and in turn chase the same or another individual. Chasing sequences sometimes extended to low branches on the trees surrounding the breeding site. At intervals, a bird would stand and lower its head in a "bow" as if briefly looking at the ground between its legs. The effect was to present the yellow crown and black ear patches to the other bird(s) in the immediate vicinity. Each "bow" was usually followed by feather ruffling and tail shaking. One interaction session lasted 5 minutes whilst each of the two others observed lasted 15 minutes. Not all birds at the site took part in this behaviour; on one occasion, two individuals remained standing on a nearby rock throughout the session.

Roosting behaviour

Roosting behaviour was variable. Outside the breeding season (February-April), birds congregated at the breeding sites in the evenings as described above but left at dusk, singly or in pairs in different directions to roost in nearby trees. This occurred in six of eight site checks. In two cases however, birds were found sleeping in breeding nests in the non-breeding season. In the Kambui Hills, two out of six nests were used in this way whilst in the Gola forest only one bird roosted at a site containing four nests.

During the breeding season (July/August), birds were found in breeding nests at night, in all five site checks made, although egg-laying had not started. However, although not all nests at a breeding site were used for roosting, all the available nests (7 in Gola, 6 in Kambui and 4 in the WAPF) were subsequently used for breeding. At certain times in the breeding season, all nests were in use simultaneously.

3.5.3. Breeding biology

Nests

All nests were cup-shaped mud structures impregnated with dried leaves, fibres and twigs (Chapter 1: Plate 1) and were similar in form to those previously described (eg Lowe, 1938; Glanville, 1954; Tye, 1987; Ash, 1991; Fotso, 1993). The majority of nests were built on overhanging rocks (73), with very few on cliffs (4) and in caves (1).

Internal nest cup size (l x b x d) averaged 10.8 x 17.2 x 12.9 cm (n=64; Table 3.2; sample sizes of variables differ due to incomplete information for some nests). There were no significant differences in mean nest cup size between different locations ($F_{5,45}$ = 1.258; $p > 0.1$, $n = 51$) but individual sizes varied widely; as much as by a factor of six for some dimensions.

Clutch size

Mean clutch size was 1.92 (n = 77). Of the 77 clutches examined, 71 were of two eggs whilst six comprised one egg.

Egg size

Egg size averaged 25.8±0.24 mm x 38.3±0.27 mm (n = 47) ranging from 20.0 - 28.0 mm x 30.4 - 42.0mm (Appendix 3.4).

Birds eggs begin to lose weight by diffusion of water vapour immediately after they are laid (Drent, 1975). However, initial (fresh laid) egg weights can be determined from linear dimensions by calculating a species-specific weight constant (K_w) from the relationship: $W = K_w l b^2$ (Hoyt, 1979), where l is length and b, breadth

Table 3.2.The dimensions of *Picathartes gymnocephalus* nests (cm) in different regions of Sierra Leone

Nest Dimension	Mean ± s.e. (n):							
	Gola Forest	Kambui Hills	Loma Mts	Kangari Hills	Dodo Hills	WAPF	All Sites	Ranges:
Internal width at rim	17.5±0.45(24)	17.2±0.25(9)	17.5±0.6(8)	17.7±0.01(7)	15.7±0.94(3)	16.4±0.56(10)	17.2±0.28(61)	9.9-21.4
Internal length at rim (front to back)	11.0±0.43(23)	10.9±0.35(4)	11± 0.43(6)	10.3±1.01(7)	9.3± 0.48(3)	11.2±0.42(10)	10.8±0.2(63)	4.4- 5.5
Internal depth	12.9±0.35(23)	12.1±0.81(7)	11.9±0.79(8)	13±1.9(7)	9.4±1.6(2)	14.8±0.83(10)	12.9±0.36(57)	4.0-20.0
External height at front	14.8±3.1(14)	21.1± 7.7(12)	12.3±3.3(7)	20±9.4(7)	13.8±6.4(3)	19.8±5.2(10)	17.0± 0.4(61)	6.0-38.8
External height at back	20.3±0.74(9)	20.2±1.06(12)	19.1±1.21(8)	23.8±3.81(7)	14.3±4.45(3)	19.1±1.73(10)	20.0±0.78(49)	7.2-43.3
Nest rim	0.99±0.06(21)	1.1±0.1 (5)		1.6±0.07 (7)	1.4±0.32(3)	1.0 (4)	1.13±0.06(40)	0.6-1.9

Missing values were not recorded

The weight constant - K_w - for *gymnocephalus* was 5.74 x 10^{-4} ± 9.5 x 10^{-6} (n = 4 eggs from 3 clutches). This was determined from eggs detected on the day of laying, for which all three measurements (*l*, *b* and *w*) were available (Appendix 3.4). The estimated mean initial (fresh laid) weight of *gymnocephalus* eggs was 14.7g ± 0.26g (range: 9.2 - 17.4g, n = 47). This was 6.71% of mean adult body weight (219.6g).

There was a decline in mean estimated fresh laid weights of clutches during the breeding season, but this was not statistically significant (Fig. 3.5 & Appendix 3.5; Spearman's rank correlation, r_s = -0.093, p > 0.5, n = 15).

Average egg weight loss during incubation was 14% of the estimated fresh weight or an average of 0.01g per day (Fig 3.6, n = 4 clutches).

Incubation

Eggs were laid one day apart and incubation began on the day the first egg was laid (n=2 nests). Estimates of the incubation period (taken as the average interval between the laying of an egg and the emergence of the young bird; Brooke, 1991) for the most closely monitored nests were from 17 - 23 days (median = 20 days)(Table 3.3.)

Nest attendance

No more than two adults were observed attending any nest at any time (n = 438 hours of observation at 17 nests).

Parents shared incubation and parental care. One bird remained at the nest whilst the other was away. Replacement of the attending adult at the nest invariably occurred simultaneously with the bird's departure. Active co-operation between attending adults (exchange of food or nesting material) was observed on several occassions.

Fig 3.5. Relation between the estimated fresh weights of *P. gymnocephalus* eggs laid in the Kambui Hills in 1993 and progress of the breeding season. Individual values represent mean weight of a clutch.

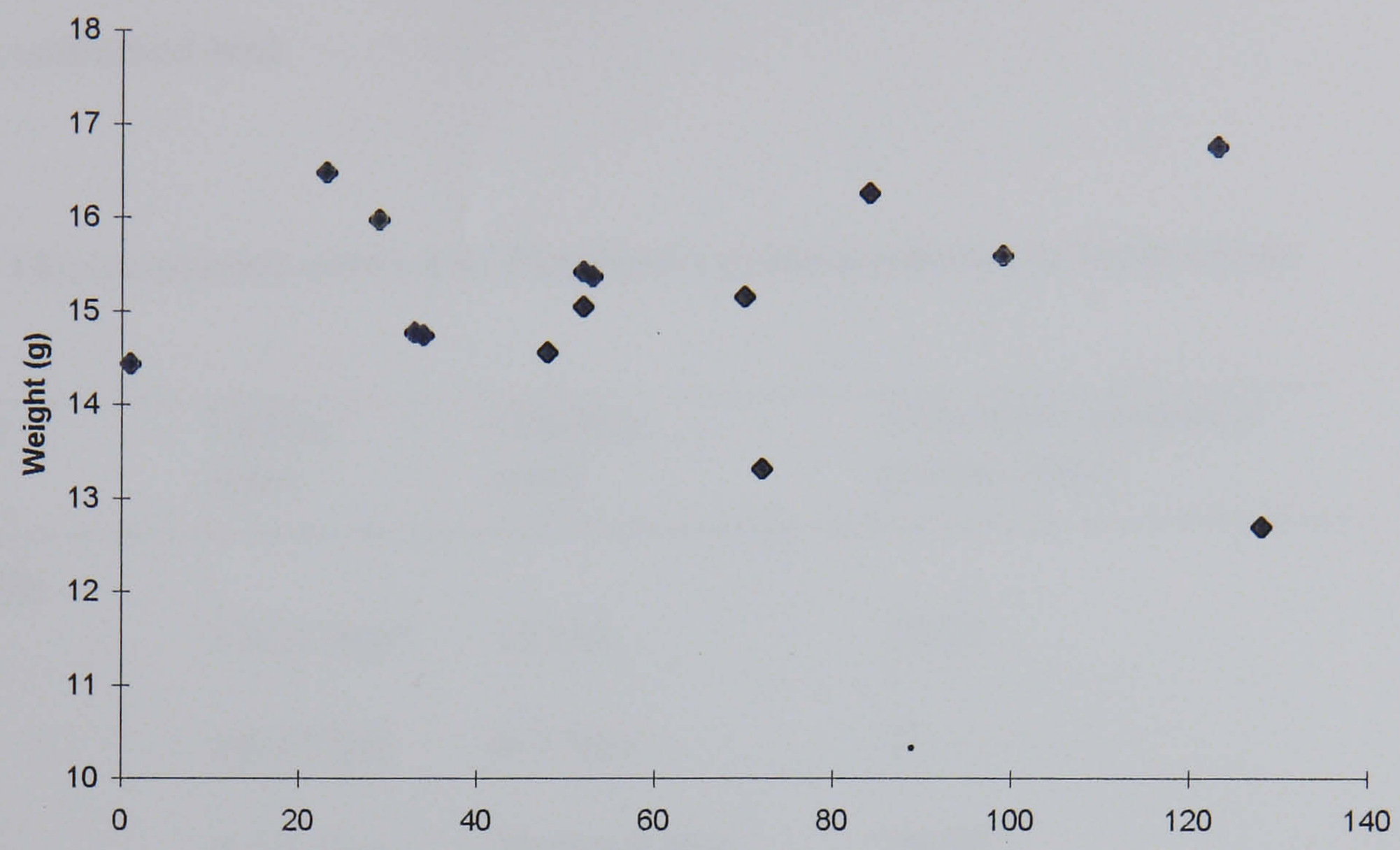
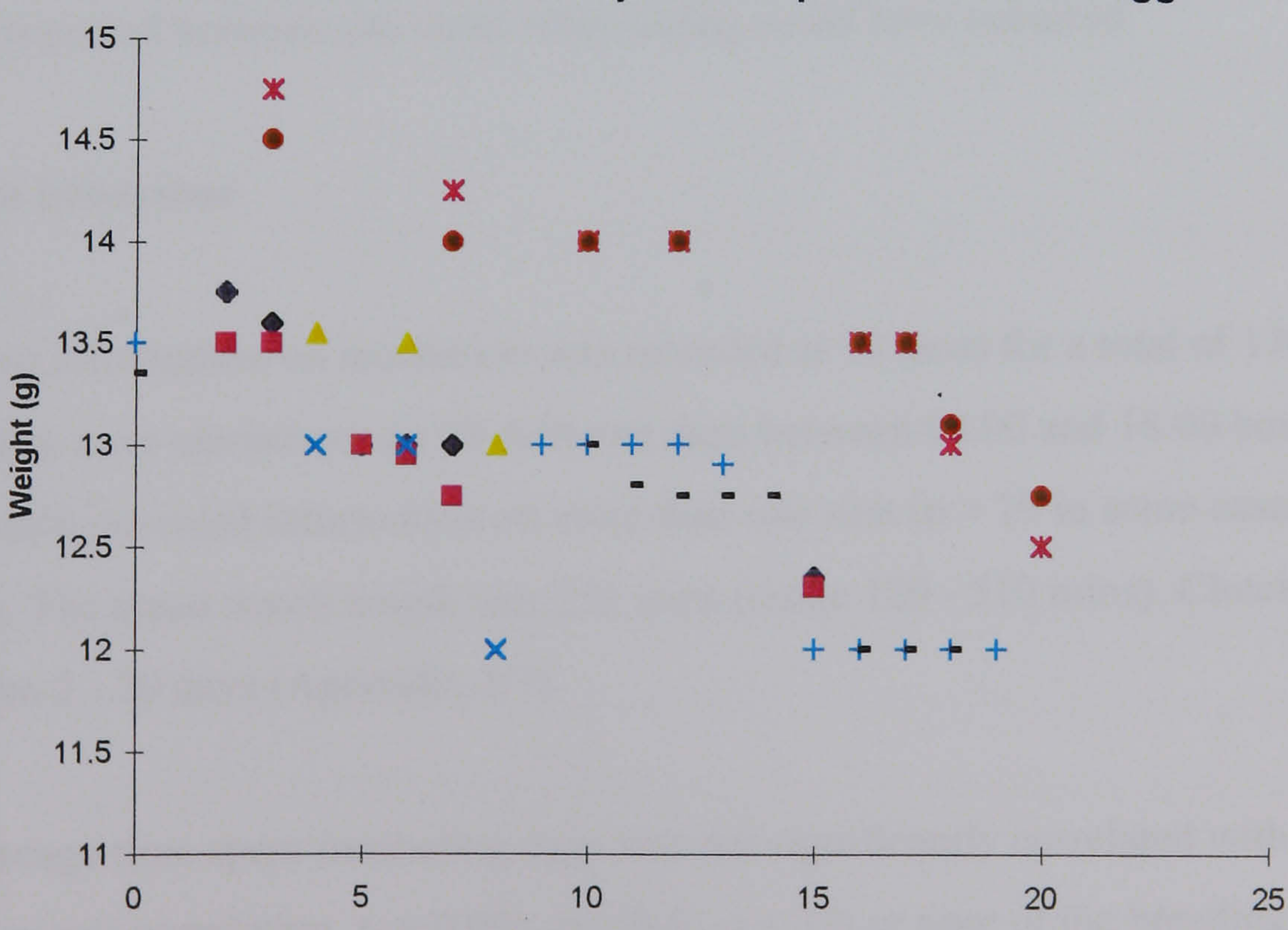


Fig 3.6. Weight loss (g) by *P. gymnocephalus* eggs during incubation. Different symbols represent different eggs



At each of four nests (three in the Kambui Hills and one in Gola), one of the attending adults had been colour-ringed prior to the start of the breeding season. All co-operative interactions observed between adults at these nests were between a marked bird and an unmarked bird.

Table 3.3. The incubation perio d of *Picathartes gymnocephalus* in Sierra Leone

Study Area and nest	Laying dates	Hatching dates	Estimated incubation period (days)
Kambui Hills			
N2a	17-21 Sep*	10 Oct	19-23
N2b	16-17 Oct	6-7 Nov	21
N4a	9-10 Oct	29 Oct-2 Nov	19-23
Gola Forest			
N2	18-20 Oct*	6-8 Nov	17-21
N3	18-20 Oct*	6-8 Nov	17-21
N6	4-9 Nov*	26 Nov	17-22

* : includes period between site visits when laying could have occurred.

Incubation behaviour

Quantitative information on incubation was recorded at 14 nests for a total of 176.7h. Nest-watches were carried out on 29 different days between 08.00 and 18.00 hours but a single watch provided information on more than one nest (n > 29 in some cases: Table 3.4). The mean watch length was 252 mins (range 120 - 510 mins). Clutch age ranged from 2 - 20 days (Appendix 3.7).

The percentage time spent incubating eggs was not significantly correlated with clutch age (Spearman's correlation, $r_s = 0.091$, $p > 0.5$, $n = 37$) or time of the breeding season ($r_s = 0.104$, $p > 0.5$, $n = 37$; Fig 3.7. and Appendix 3.7.). Also, there was no

significant difference between incubation constancy on one-egg and two-egg clutches (Mann-Whitney U = 10.0; p > 0.6, n = 11 nests; Appendix 3.7.)(nests at which only single watches were made were excluded from the analysis). Similarly incubation constancy was not significantly different between nests in which both eggs hatched and those in which at least one egg was lost (Appendix 3.7; Mann-Whitney U = 7.0, p = 0.143, n = 11 nests).

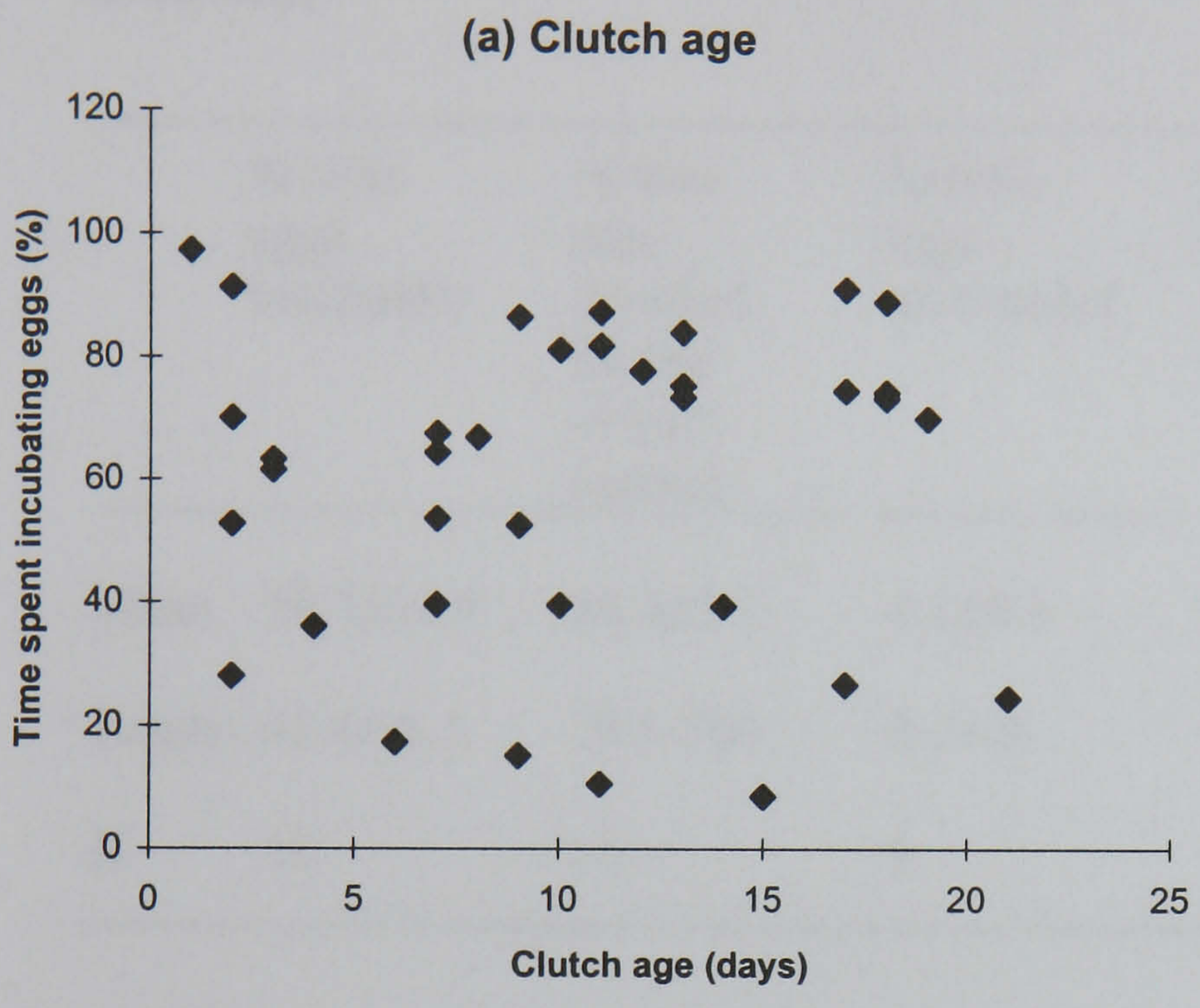
Overall incubation constancy (pooled data for all egg ages and clutch sizes) was 59.4% (Table 3.4). Incubation bouts lasted approximately 60 mins with each bout consisting of three discrete stints per hour on average. Mean stint duration was 12.6 mins and intervals between each stint lasted about 8 minutes (Table 3.4) during which time the bird either perched on the nest rim,on a nearby branch, or stood on the ground outside the nest. Nests were attended by one or both parents for 96% of observation time (173 h).

Parents attending a nest could not be distinguished by sex, but relative parental time investment in incubation could be assessed at a nest at which one of the attending birds was ringed (N5 - Kambui Hills)(Table 3.5; Appendix 3.8a.). The two parents (*w y* and *u m*) spent almost equal amounts of time at the nest (41.6% and 45.1% of the total observation time respectively) but one of them (*w y*) incubated the eggs for significantly shorter periods at a time (Mean stint durations = 6.5±1.29 mins and 24.7±6.38 mins respectively; Mann-Whitney U = 58; p < 0.01). However, this bird (*w y*) performed more than twice as many stints per hour (2.2) as its unmarked partner (0.92: Table 3.5)

Hatching

Hatching was asynchronous. Eggs in the same clutch hatched at least 12 hours apart. Eggshells were removed from the nest by attending adults within one hour of hatching and deposited in bushes around the breeding site. Eggshell pieces remaining in the nest were eaten.

Fig 3.7. Relation between the percentage time *Picathartes gymnocephalus* adults spent incubating and (a) clutch age and (b) progress of the breeding season Each plotted point is from a watch of one nest. Mean watch length was 252 mins.



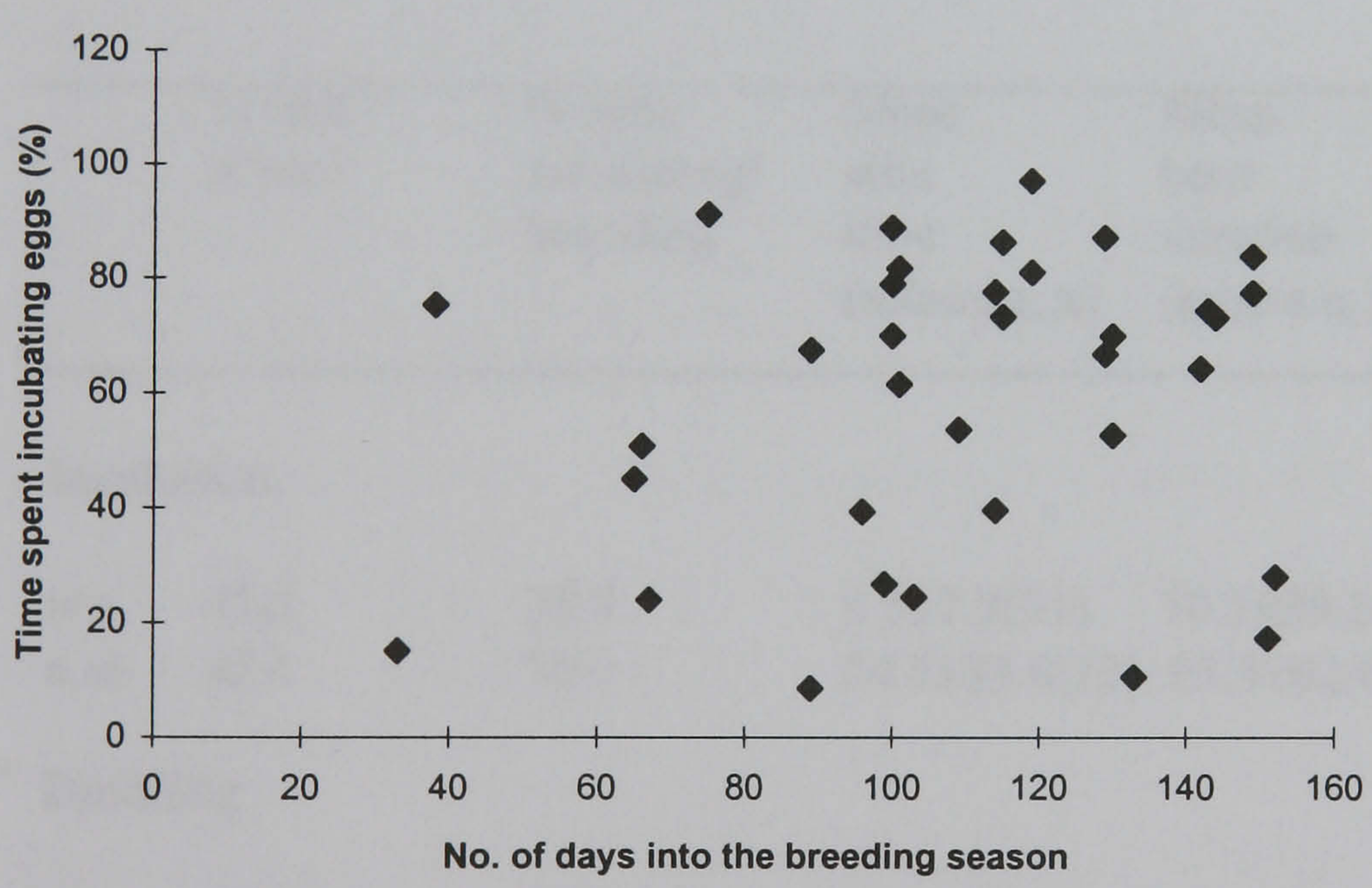


Table 3.4. Quantitative indices of *Picathartes gymnocephalus* incubation behaviour.

	% time eggs incubated	% time nest attended by one or both parents	% time eggs unattended	Mean bout duration (mins)	Mean stint duration (mins)	Mean interval between stints
Mean	58.7±14.9	96.3±7.7	4.1±8.1	59.3±45.1	11.6±5.7	8.4±5.3
Range	41.4-85.1	78.1-100	0-21.9	5-146	4.7-23.1	3.2-19.6
N	10	10	9	9	10	10

Table 3.5 Relative parental time investment in egg and nestling care by *Picathartes gymnocephalus* in the Kambui Hills

	% time at nest	% time incubating/ brooding	Mean stint time (min±s.e, n)	Mean bout duration (min±s.e, n)	No.of stints per hour
Incubation					
w y	41.6	23.9	6.5±7.2(31)	70.3±39.2(5)	2.2
u m	45.1	38.0	24.7±23.0(13)	63.5±62.6(6)	0.92
Brooding					
w y	21.2	10.6	4.3±4.7(21)	25.9±22.4(7)	1.5
u m	40.6	23.4	10.0±7.9(20)	43.4±39.7(8)	1.4

w y: white and yellow rings; *u m*: unmarked

The nestling period

The mean nestling period (the average interval from hatching to a young bird leaving the nest) was 25.3±2.65 days (n=6 nests; 23 days at three nests, 27 days at two nests and 29 days at one nest). Nestling periods were determined from nests at which nestlings left the nest at least 12 hours after a nest inspection.

Brooding

A total of 31 nest watches were made at 7 nests from 27 October to 27 November 1992 and 15 August to 17 November 1993. These watches averaged 3 h 59 mins (range 138 - 377 mins), with each providing information on 1 - 3 nests, so that n was greater than 31. Nestlings observed ranged in age from newly-hatched (day 0) to 25 days old (median age: 6 days) (Appendix 3.9).

Newly hatched nestlings were brooded for as much as 86% of observation time (Fig 3.8). Brooding then declined as nestlings grew older and nestlings more than 13 days old were not brooded at all (Spearman's correlation, $r_s = -0.609$). The time of the breeding season apparently did not influence brooding behaviour as there was no significant correlation between progress of the breeding season and time spent brooding (Appendix 3.9; Spearman's correlation, $r_s = -0.275$; $p > 0.275$).

At N5 in the Kambui Hills, relative parental time investment in brood care followed the same general pattern as during incubation (Table 3.5, Appendix 3.8b) with significantly less contribution from the ringed parent than its partner (observed nestlings were 2 - 13 days old). The difference in mean brooding stint durations between the parents was statistically significant (Mann-Whitney U = 97, $p < 0.005$, n = 20,20), but that for mean bout durations was not significant (Mann-Whitney U = 39, $p > 0.2$, n = 8,7).

Fig 3.8. The relation between the amount of time spent brooding and nestling age in *Picathartes gymnocephalus*

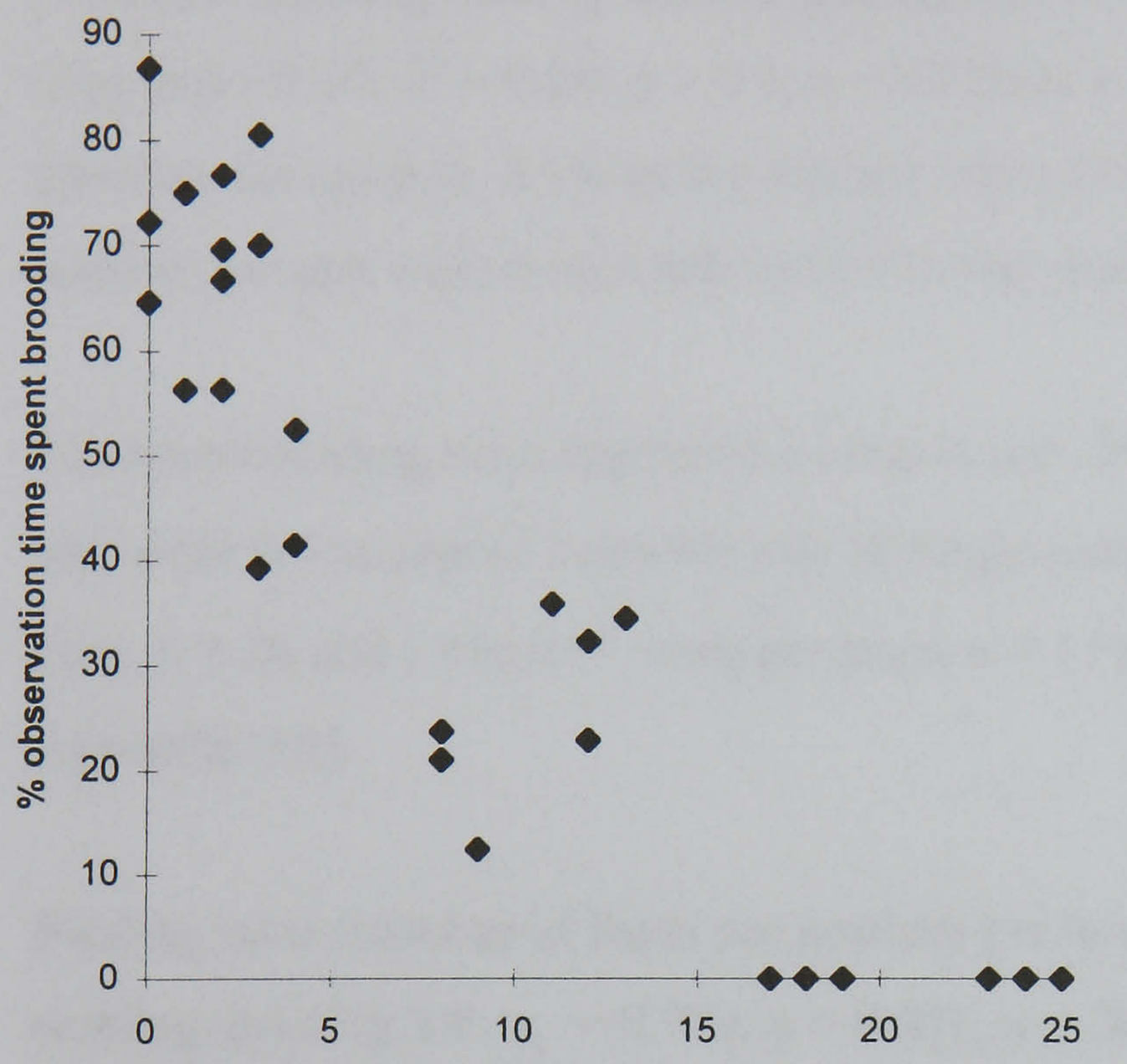
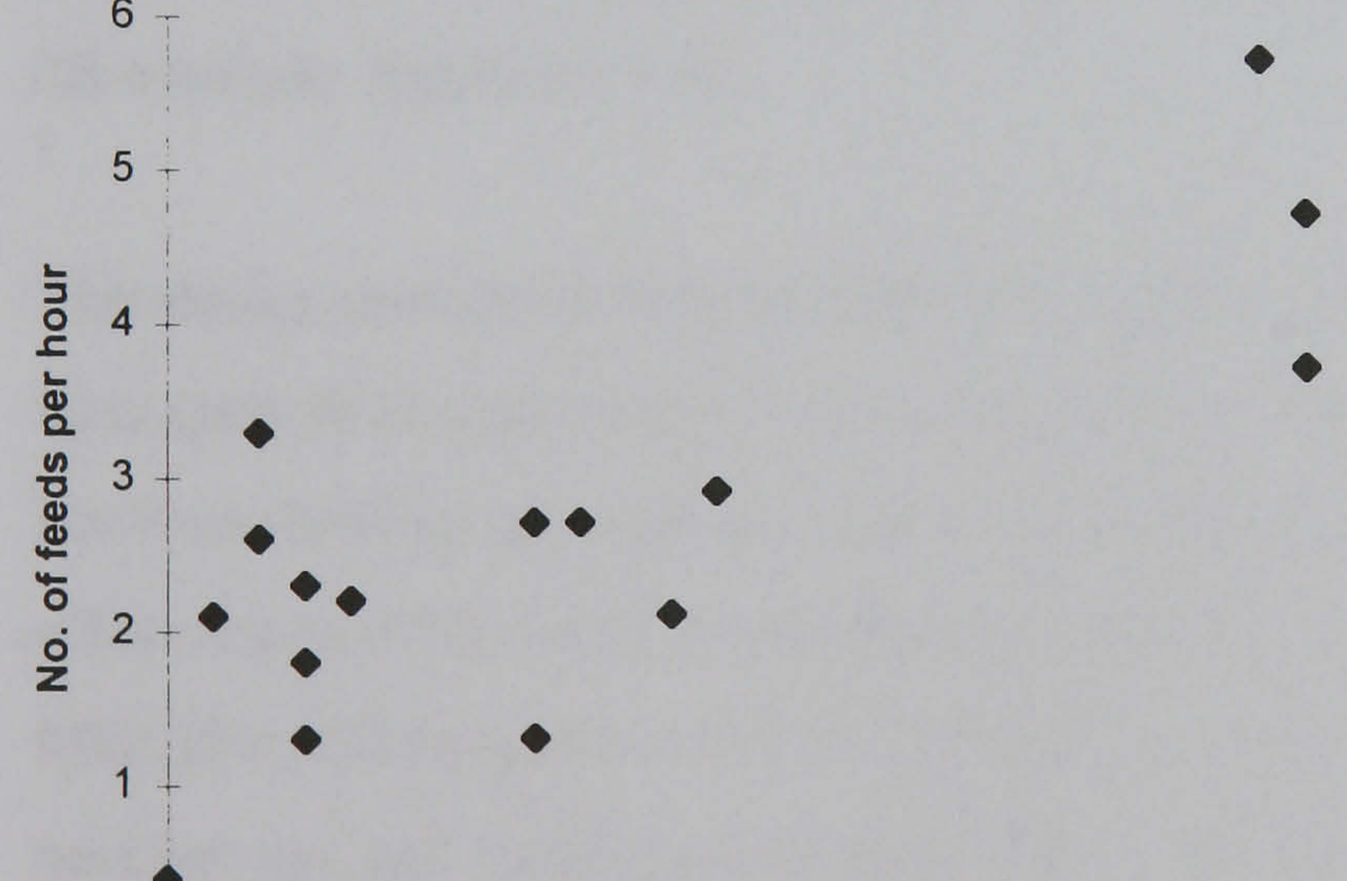


Fig 3.9. Relation between the provisioning rate of *P.gymnocephalus* nestlings and their age (all broods = 2 nestlings)



Food provisioning

Food provisioning rates by attending adults did not differ significantly from a 1:1 ratio (Appendix 3.10: $X^2 = 0.24$; $p > 0.5$; $n = 98$ feeds in 42 hours at two nests). Food transfers occurred in 3.1% of the feeding trips; from a ringed parent to an unmarked adult at the nest who in turn delivered it to the young.

Food provisioning rates depended on brood size. Broods of two nestlings (1 - 9 days old) were fed at almost twice the rate of single-nestling broods (2.79±0.23 feeds per hour, $n = 26$ and 1.48±0.17 feeds per hour, $n = 17$ respectively; $t_{40} = 4.575$, $p < 0.001$: Appendix 3.9).

Feeding rates (number of feeds per nestling per hour) were positively correlated with nestling age (Fig 3.9: $r_s = 0.780$; $p < 0.001$, $n = 28$ watches) and increased from less than one feed per hour for newly hatched nestlings to 2.85 feeds per nestling per hour for nestlings 24 days old.

As with incubation and brooding behaviour, the time of breeding did not appear to influence food provisioning behaviour; there was no significant correlation between the time of the breeding season and food provisioning rates ($r_s = -0.113$, $p > 0.5$, $n = 28$ watches: Appendix 3.9).

The strong correlation between nestling age and food provisioning rates as well as time spent brooding (see previous section) could have been due to an association between nestling age and the time of the breeding season. However, when the latter effect was partialed out (using the "residual correlation matrix") from the module MGLH in the program SYSTAT) (Wilkinson 1990); partial correlations between nestling age and food provisioning rates ($r = 0.758$) and time spent brooding ($r = -0.869$) remained highly significant.

Parental Defence

Breeding adults chased off conspecifics which approached their nests to distances less than the minimum internest distance (1.5 - 2.0m). The maximum recorded distance at which an attending adult attacked an intruder was 3m. Fights were recorded in 3.2% of aggressive encounters (n=62). Aggressive interactions increased from 0.087 per hour for all observations in the egg stage to 0.25 in the nestling stage and showed a significant positive correlation with nestling age (Spearman's correlation, $r_s = 0.432$, $p < 0.05$, $n = 27$; Table 3.6, Appendices 3.7 & 3.9). However, nests were left unattended for 3.8% and 2.5 % of total observation time during the egg and nestling stages respectively (Table 3.6; Appendices 3.7 & 3.9). There was no significant difference in the percentage time a nest was left unattended between nests in which both eggs hatched and nests in which at least one egg was lost (Mann-Whitney $U = 17$, $p = 0.17$, $n = 10$ nests). Similarly in the nestling stage, although there was less data, there was no significant difference in the percentage time nests in which both nestlings fledged were left unattended and nests in which at least one nestling was lost (Mann-Whitney $U = 1.0$; $p > 0.1$; Appendix 3.9).

Table 3.6. Parameters of nest defence by *Picathartes gymnocephalus* presented as mean, standard error (n) and range.

	Time nest left unattended (% of observation time)	No. of aggressive acts per hour
Incubation	3.8±1.4 (37)	0.087±0.04(42)
Range	0 - 34	0 - 1.26
Nestling stage	2.5±0.93 (37)	0.25±0.07 (44)
Range	0 - 20	0 - 2.67

Nestling development

Previous descriptions of the development of nestling *P. gymnocephalus* have not covered the whole nestling period (Glanville,1954; Grimes, 1964; McKelvey,1981; Tye 1987; observations for less than a week in all cases). I examined development in

nine nestlings (from five nests) on 17 days distributed between the beginning, middle and end of the nestling period.

Nestlings hatched naked except for three to four bristles on the crown which persisted into adulthood and a single row of white down along the spine. The eyes were closed and there was no sign of the conspicuous black parietal patches characteristic of adults. The body was translucent pink below and light brown above with black wing buds. This agrees with previous descriptions given by McKelvey (1981) and Tye (1987).

Primary and secondary quills began to grow two to three days after hatching (n = 4 nestlings). The eyes opened on day four (one-third open when gaping, otherwise closed). The rectrices and tertiaries appeared on days five to six when the longest primary was about 4mm long. By day seven, wing covert quills had emerged and pins had appeared on all the main body pterylae (spinal, thoracic, abdominal, lateral and scapulo-humeral). The ear patches were distinct but were light brown or flesh-coloured. The bill was pale brown (almost "yellow") with a white rim and there was a black patch around each eye. The legs were pale grey.

Begging calls were first heard on day eight. At this stage, nestlings stretched their necks upward and gaped widely in response to touch on the nest or body. Nestlings defaecated over the rim of the nest as from eight to nine days old. Prior to that age, faeces deposited in the nest were either eaten or removed from the nest by the parents.

The primaries, secondaries and rectrices burst from pin on days 11 - 12. Ventral and lateral body tract feathers consisted of yellowish-white down. The body was still mostly naked with wide apteria on dorsal and ventral surfaces. By day 15 to 16, feathers on all the main pterylae were also out of pin. The bill was now black with a yellow gape and the interior of the mouth bright orange-yellow. The ear patches were distinct as grey patches on a dark brown crown and the legs were light blue.

The first signs of yellow appeared on the dark brown crown at the end of the third week. By day 23, the crown was almost completely pale yellow with isolated smudges

of black mostly at the centre. On day 25, just prior to fledging, nestling plumage closely resembled that of the adult; mainly black above and white below with a lemon-yellow wash on the throat and upper breast; yellow skin on the head contrasted sharply with black ear patches. However, the yellow crown of the nestling was slightly paler than an adult's and there were no down feathers below the contour feathers on the dorsal surface. Also, the upper legs in the region of the femur were virtually naked except for pins on the crural tract.

Nestlings more than three weeks old, regularly stood in the nest or climbed on the rim to preen or flap their wings.

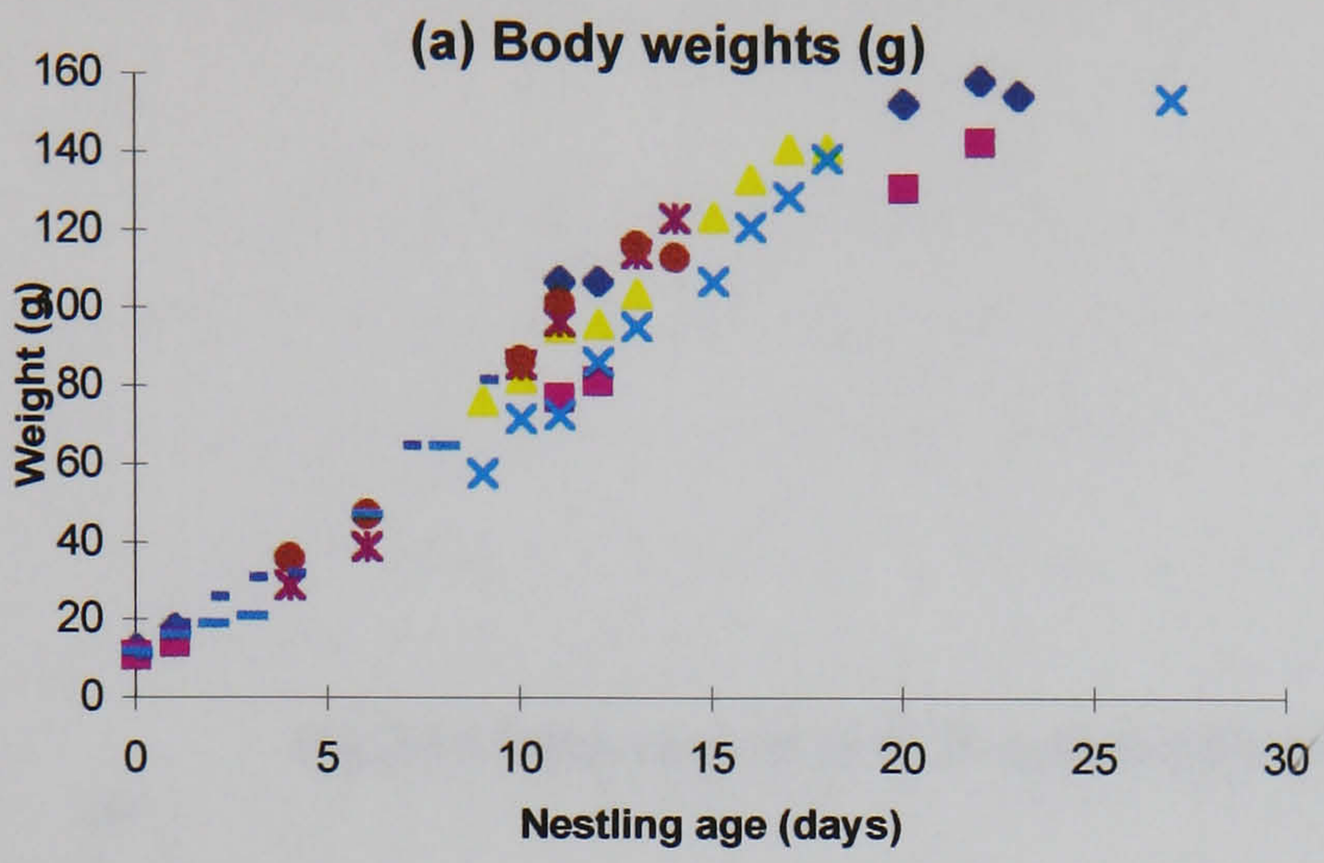
Nestlings about to fledge whistled in a characteristic piercing manner as previously noted by Grimes (1963, 1964). Young birds left the nest by gliding with oustretched wings from the nest rim. Each fledgling was met by an adult which actively led it away. In two of three cases, the adult also produced the characteristic whistle and brought insects to the young bird whilst moving further away from the breeding site. In two of three cases, the fledglings were quite weak and stumbled repeatedly as they moved away.

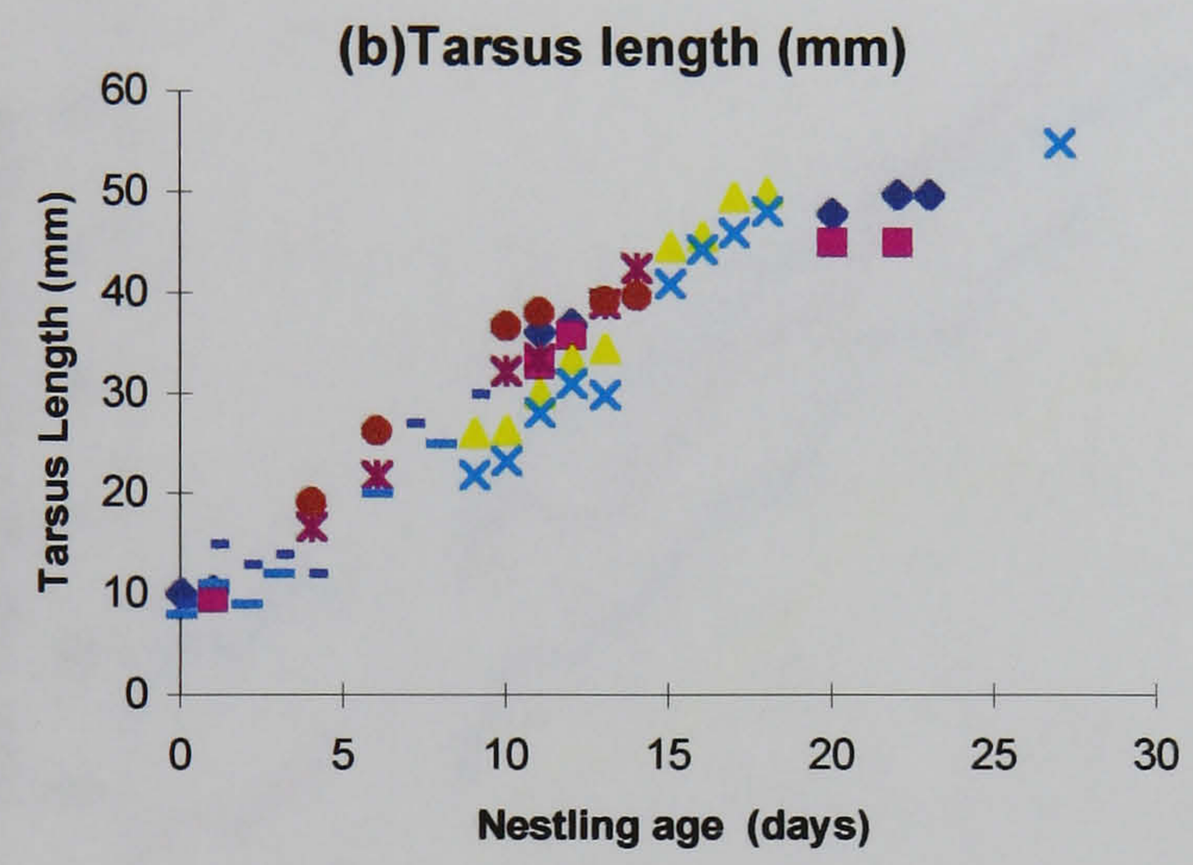
Nestling growth

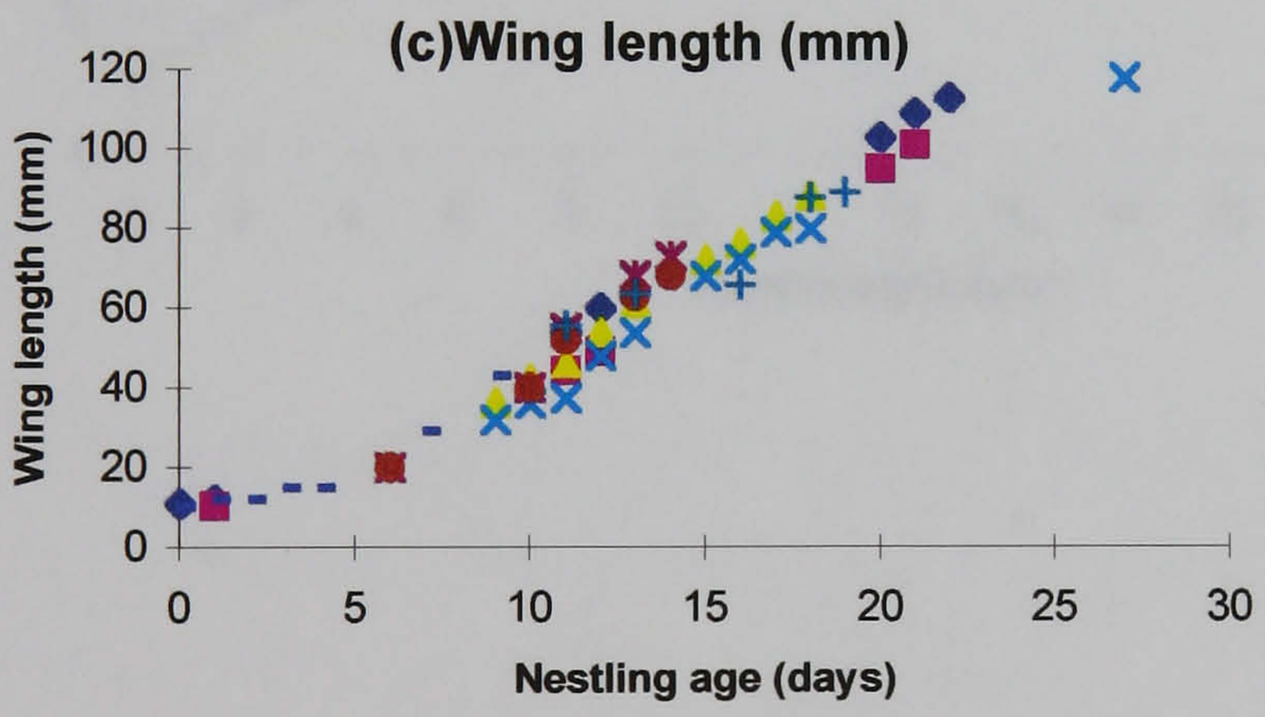
Body measurements and weights, of nine nestlings (from five nests), with known hatch dates were recorded from the day of hatching (day 0) to day 26 (n = 250 measurements; sample sizes of variables differ due to incomplete information for some birds on some days). Hatchlings had a mean weight of 11.6±0.7g (n=4; Fig 3.10.). This was 5.2% of the mean weight of an adult (219.2g) and 76.5% the weight of a fresh egg (14.9g). Mean hatchling wing, tarsus and bill lengths, with s.e. were 10.3±0.6mm; 9.0±1.0mm and 8.3 ±1.5 mm respectively (n = 3 in each case).

Mean measurements (n=2) on the day before fledging (day 26), with their percentages of mean adult measurements, in parentheses, were weight of 155.5±0.7g (72 %); wing length of 115.5±3.5mm (71 %), tarsus length of 52.5±3.6mm (84 %) and bill length of

Fig 3.10: Growth curves of weights and body measurements of *Picathartes gymnocephalus* nestlings (different symbols signify different nestlings)







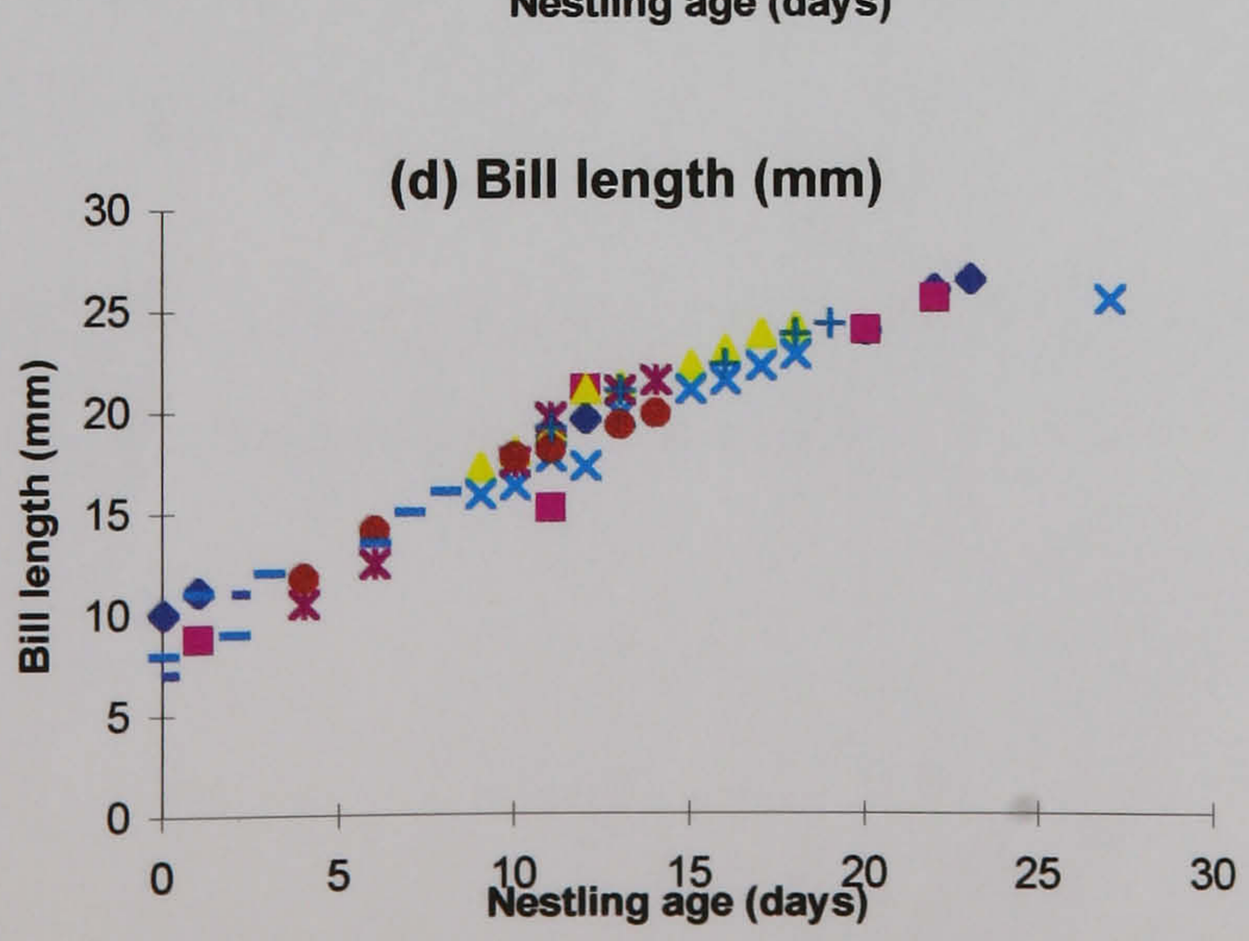
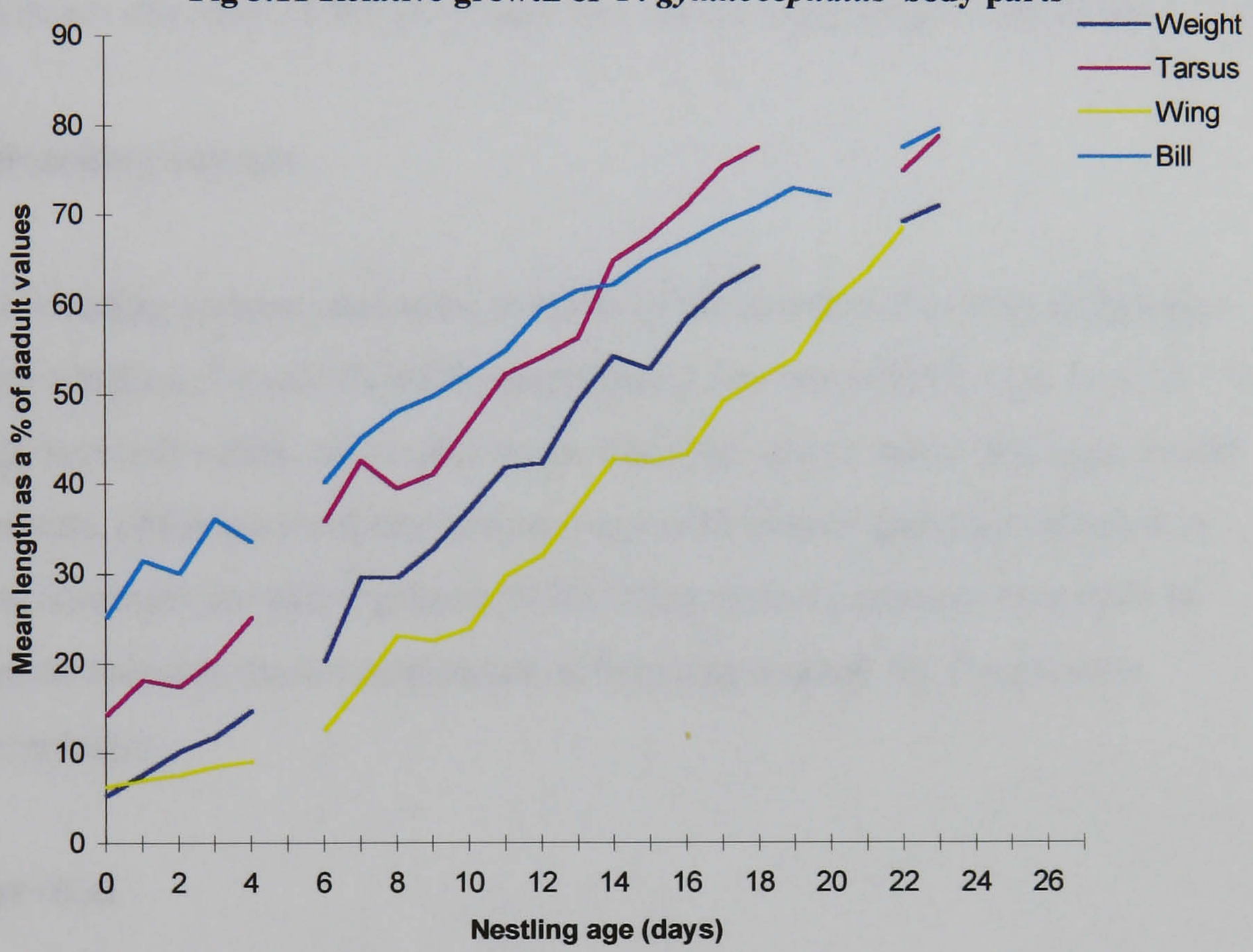


Fig 3.11 Relative growth of *P. gymnocephalus* body parts



26.0±0.7mm (79 %) (Figs 3.10 & 3.11). Tail length (5.0±2.8mm, n = 2) was less than one-third the length of that of a mature adult (18.3mm).

The tarsus grew fastest of all measured parameters (Fig 3.11). The greatest absolute increase in body measurements took place after 23% of nestling time, that is after day 6. The daily mean weight gain was 4.8±2.3g during the first week of growth but doubled to 8.3g during the second and third weeks. Two- and three-week old nestlings averaged 110.8±10.5g (n = 5) and 143±15.5g (n=2) in weight respectively. Growth slowed down after day 18 for all parameters except wing length (day 21)(Fig. 3.11).

3.5.4. Breeding success

Annual breeding success measured in terms of the number of young fledged per breeding adult can be calculated by determining the mean clutch size, nest survival rate, egg survival within successful nests, hatching rate of surviving eggs, brood survival rate, chick survival rate within successful broods and mean number of breeding attempts per pair (Jackson 1988). This section presents the results of attempts to measure these components of breeding success for *Picathartes gymnocephalus*

Egg survival

A total of 55 breeding attempts were monitored between 1990 and 1994 (n = 100 eggs). The average Mayfield egg survival rate (assuming a 20-day incubation period) was 45.3% with 95% confidence limits of 36% to 56.9% (Table 3.7 & Appendix 3.12a). Daily mortality averaged 3.9% per day (range = 1% - 6.8%).

Average egg survival at each site, varied widely between years (by as much as a factor of two), except in the Kambui Hills (Table 3.7).

Nestling Survival

Thirty-nine nestlings at 24 nests monitored over 587.5 nestling-days in three years had an average survival rate of 50.4% during a 25-day nestling period, with 95% confidence limits of 32.5% to 68.5% (Table 3.8 & Appendix 3.12b). Data for survival rates during the nestling period at different sites between 1990 and 1994 are shown in Table 3.8. Average daily mortality rate was 2.7% ranging from 0.4% per day at Baiama in the Kambui Hills in 1993 to 6.4% per day at the same site in 1992.

Table 3.7. Survival rates of *Picathartes gymnocephalus* during the incubation period

Site and Year	No. eggs (nests) obs.	No. eggs lost	Exposure (egg-days)	Daily mortality rate (*dmr*)	Daily survival rate (*dsr*)	SE* of *dsr*	Average survival rate (*asr*)
Gola							
1990	18(12)	10	268.5	0.037	0.963	0.012	0.468
1992	21(11)	13	191.5	0.068	0.932	0.018	0.245
Kambui							
1992	12(7)	7	179	0.039	0.961	0.014	0.45
1993	25(13)	12	291.5	0.041	0.959	0.012	0.431
WAPF							
1990	8(4)	4	114	0.035	0.965	0.017	0.490
1994	16(8)	2	192	0.010	0.990	0.007	0.811
All Sites							
	100(55)	48	1236.5	0.039	0.961		0.453

Table 3.8 Survival rates of *Picathartes gymnocephalus* during the nestling period.

Site and Year	No. nestlings (nests) obs.	No. lost	Exp. (nestling-days)	DMR	DSR	SE* of dsr	ASR
Gola							
1990	8(4)	4	130	0.031	0.969	0.015	0.459
Kambui							
1992	6(4)	2	31	0.065	0.935	0.044	0.188
1993	11(6)	1	238.5	0.004	0.996	0.004	0.905
WAPF							
1990	4(3)	2	59.5	0.034	0.966	0.023	0.421
1994	10(7)	7	128.5	0.054	0.946	0.020	0.250
All Sites	39(24)	16	587.5	0.027	0.973		0.504

* Standard errors were underestimated because fates of individual eggs and chicks were underestimated.

Survival from start of incubation to fledging

The probability of *gymnocephalus* eggs surviving both the incubation and nestling periods was 22.85% (Tables 3.7 & 3.8). Average survival rates at all the study sites were quite similar (22% in Gola, 23.5% in the Kambui Hills and 20.5% in the WAPF). In the WAPF, average survival rates in 1990 and 1994 were almost the same (21% and 20% respectively; Table 3.9) whilst in the Kambui Hills there was a marked difference in survival between 1992 (8.5%) and 1993 (39%). Low survival in 1992 was due to very high nestling mortality (81.2%: Table 3.9) which subsequently dropped markedly in 1993 (9.5%). Similar wide fluctuations in nestling mortality occurred between years in the WAPF (from 42% in 1990 to 25% in 1994). However, unlike the situation in the Kambui Hills where egg survival remained almost the same between years; in the WAPF, a corresponding change in egg survival in the opposite direction to that of nestling survival, meant that overall survival remained almost constant.

Survival during the incubation and nestling periods were significantly different in the Kambui Hills in 1993 ($p < 0.001$) and in the WAPF in 1994 ($p = 0.0183$) but these variations did not show any clear pattern (Table 3.9). In the Kambui Hills in 1993, eggs suffered significantly higher mortality than nestlings but the opposite was the case in the WAPF in 1994. However, when averaged across all sites for which data were available for both periods during a particular year, survival rates during the incubation and nestling periods were essentially the same (50.6% and 50.4% respectively: Table 3.9).

Table 3.9: Estimated survival rates of *Picathartes gymnocephalus* during incubation and nestling periods at different sites in Sierra Leone

	Gola Forest	Kambui Hills		WAPF		All sites
	1990	1992	1993	1990	1994	
Incubation	0.468	0.45	0.431	0.49	0.811	0.51
Nestling period	0.459	0.188	0.905	0.42	0.25	0.50
Both periods	0.22	0.085	0.39	0.21	0.2	0.26

Table 3.10: The average number of *Picathartes gymnocephalus* young fledged per breeding attempt.

Mean clutch size	1.92 (n = 77 clutches)
Egg survival rate (from Table 3.7)	0.453
Mean no. of chicks produced per pair	0.87 (0.453 x 1.92)
Nestling survival rate (from Table 3.8)	0.504
No. of chicks fledged per pair	0.439 (0.87 x 0.504)

Productivity

The components of *gymnocephalus* productivity are summarized in Table 3.10. Total number of chicks fledged per adult was 0.22.

Causes of mortality

Predation

Depredation was assumed to have occurred at nests at which the two eggs or chicks were lost simultaneously without trace. This was the main cause of nest content losses (41%:, n = 22 nests; Table 3.11).

Potential predators were snakes (the Spitting Cobra , *Naja nigricollis* and Black and White Cobra, *Naja melanoleuca*) and monitor lizards (*Varanus niloticus*) which were flushed from below *gymnocephalus* breeding sites on separate occassions; forest sun squirrels (*Heliosciurus* spp), forest raptors (eg West African Goshawk, *Accipiter toussenelii*) and Colobine monkeys which elicited strong anti-predator reactions (mobbing, alarm calls , visible agitation or frozen postures) from breeding *gymnocephalus*. Also, two young boys were seen with two *gymnocephalus* eggs in the Kambui Hills on one ocassion.

Infertile eggs

Eggs which remained in the nest beyond the maximum estimate of the incubation period before disappearing were deemed inviable. This accounted for 9% of nest content losses (Table 3.11).

Infanticide and competition

Infanticide and/or competition from conspecifics caused 13.6% (3) of nest content losses (Table 3.11). In two cases, an unmarked adult removed three-day old nestlings, and eggs at the end of the incubation period respectively from their nests. The

nestlings were unattended at the time and a parent brought a worm to the nest ten minutes after the incident. In the case of the destroyed eggs, the apparent intruder, inspected two unoccupied nests before removing the nest lining and two eggs from the third nest.

Table 3.11. Numbers of *Picathartes gymnocephalus* nests lost in different ways during incubation and the nestling period

Cause of nest loss	No. of losses (n=22)
All nest contents lost without trace	9
All nest contents lost but egg shells observed below nest	4
Nest contents lost in stages	4
Loss due to conspecifics	3
Eggs failed to hatch	2

Table 3.12 Interval (days) between successive *gymnocephalus* clutches at nests used more than once in a year. Each interval is the period between the failure date of one clutch and the beginning of egg laying of the next.

Site	Nest	Year	No. of clutches	Intervals between clutches (days)
Kambui Hills	Ba-n1	1992	3	4 7
	Ba-n4	1993	2	31
	Ba-n6	1993	2	62
	Ba-n7	1993	5	15 13 13 21
WAPF	Jb1-n1	1994	2	18

An attempt to approach a nest containing a single nestling was prevented by the apparent nest-owner . In the third case, intense fighting between nest-owners and two other adults resulted in destruction of the nest and loss of two nestlings.

Unknown mortality factors

Nests at which losses were accompanied by the presence of egg-shells below the nest (4; 18%) or in which eggs were lost one after another (4; 18%) could not be assigned to any category with certainty (eggs could have been depredated or removed from the nest by parents after failing to hatch)(Table 3.11).

Factors influencing nest mortality

The height of a nest above ground or its distance from the nearest access point from the ground could influence its susceptibility to predation. Also, variations in environmental conditions (e.g. food supply) with progress of the breeding season could mean that mortality rates would change with laying dates. The possible effects of nest-height above ground and laying dates on average daily mortality rates at different nests were therefore investigated using multiple regression analysis (the dependent variable was the fate of a nest - 0 = success, 1 = failure – divided by the number of exposure days). Data from sites between which average mortality rates were not significantly different were used in the analysis to minimise the confounding effect of different mortality rates at different sites in different years. Also all nests used in the analysis had a clutch size of two. Neither of the two fitted variables had a significant effect on mortality rates at individual nests ($F_{3,31} = 0.489$, $P > 0.5$).

Multiple nest use

Nest use by breeding pairs was analysed at 21 nests. Multiple nest use could indicate double-brooding or the laying of replacement clutches. At most of the nests (16; 76.2%), only one clutch was laid during the year. Two clutches were laid at three nests (14.2%) whilst three and five clutches were laid at one nest each (Table 3.12).

At the two nests at which three and five clutches were laid, all the clutches except one (the last of five clutches) failed. At the three nests at which two clutches were laid in a year, all clutches at two of the nests were successful, whilst both clutches at the third nest failed. The mean interval (in days) between successive clutches was 20 days (range = 4 - 61, Table 3.12).

3.6. DISCUSSION

Biometrics

Body measurements are fundamental taxonomic characters of birds. This study provides the largest sample sizes available on *Picathartes gymnocephalus* measurements in the literature to date (n = 25). Previous records were based on six specimens (Bannerman, 1948). Also, differences in tarsal length discovered in this study should prove useful in distinguishing between the sexes of birds caught in the field, in any future research and/or management of *Picathartes* (Table 3.1).

Pre-breeding behaviour

The most striking feature of the behaviour of *P. gymnocephalus* prior to breeding was the group interaction behaviour observed in the Kambui Hills in July and August in which several birds engaged in mutual bowing displays. Similar behaviour was observed by H. Mudd and R. Martins in the Cote d'Ivoire in 1991 (pers. comm.). A single individual was seen performing a behavioural pattern (repeated three times in 30 minutes) which included a deep bow with raised and partially open wings whilst facing a roosting cave entrance around which several other *gymnocephalus* were gathered. Mudd and Martins were uncertain whether the behaviour observed was that only of a particular individual, or a formalised display associated with either roosting or breeding. The observations described in this study suggest the latter explanation is more likely. The timing of the occurrence of the behaviour (immediately prior to breeding in Sierra Leone and whilst breeding was going on in Cote d' Ivoire) indicate

that its significance is probably associated with breeding. Further interpretation is not possible on present evidence.

Several authors have suggested that each pair of *Picathartes* uses one nest for breeding and another for roosting at the same colony (Glanville 1954, Grimes 1964, Grimes and Darku 1968), so that numbers of nests were double the numbers of breeding pairs present. Observations in this study showed simultaneous use of all nests in a colony by different pairs (Section 3.5.2). If the situation observed in this study is widespread, this would mean that some previous assessments of *Picathartes* populations based on one breeding pair using two nests at a colony (eg Collar and Stuart 1985; Allport 1989) may have been underestimates.

Breeding biology

My findings on the parameters of the breeding biology of *Picathartes gymnocephalus* are similar to the average for tropical passerines with respect to clutch size (1.92 and 2-3 respectively; Lack, 1968) and egg mass loss during incubation (14% and 15-16% respectively; Drent, 1975). But average hatchling weight of *gymnocephalus* as a percentage of inital fresh egg weight (76.5%) is higher than the average for birds in general (65%; Ashkenazi and Yom-Tov, 1997). This is perhaps because mean initial egg weight of *Picathartes* was estimated from linear dimensions using a species-specific weight constant (K_w) derived from a sample (n =4; Section 3.5.3.). K_w may have been underestimated because of the small sample size.

Previous estimates of the incubation and nestling periods for *Picathartes* are broadly consistent with the results of this study. The incubation period of *gymnocephalus* has been previously given in the wild as 24±1 days (Grimes and Darku, 1968); and in captivity as 23 days (Dekker, 1973) and 25 days (McKelvey, 1981). These values are slightly higher than the median of 20 days obtained in this study (Table 3.3). Fotso (1992) estimated the incubation period of *oreas* in natural populations as lasting 21 - 24 days whilst Faust (1971) obtained 20 days as the incubation period of a captive individual.

The nestling period of *oreas* (Fotso, 1992) and *gymnocephalus* (Grimes and Darku) has been previously estimated as 26 days which agrees very well with the 25.3±2.7 days determined in this study. This comparison also shows the close similarity in the breeding biology of the two *Picathartes* congeners.

Estimates of *gymnocephalus* incubation period (20 days) and nestling period (25 days) are higher than is usually the case for passerines (12-14 days and 10-20 days respectively; del Hoyo *et al*, 1992). Life history features of birds are generally related to their body size; the larger the species the greater the tendency to a "K - selected" life history strategy, with long life, deferred age of first breeding, long breeding cycle and few offspring . *Picathartes* is one of the largest tropical passerines and this may partly explain its longer than average breeding period.

In captivity, juvenile *P. gymnocephalus* remain dependent on their parents for 14 days after leaving the nest (Dekker 1973). The results from this study indicate that there is a similar period of dependence in natural populations. Nestlings fledged whilst still almost 30% smaller than adult size (Fig 3.11); some were still very weak and at least initially, they were fed by their parents.

Assuming that post-fledging dependence in the wild is also two weeks and using the estimates of the incubation period (median - 20 days) and nestling period (25 days) obtained in this study, then the period from laying to full independence in *gymnocephalus* lasts 60 days or two months.

Parental Care

In this study, *P.gymnocephalus* adults shared incubation and nestling care duties. Parents spent almost equal amounts of overall time at the nest and fed the nestlings at equal rates, but at each of two nests attended by a ringed adult and an unmarked bird, the latter spent twice as much time incubating and brooding nestlings as the former. It was also observed at these nests that it was the ringed parent that offered food to the unmarked partner in food transfers (Section 3.5.3.: Food provisioning). In many

passerines it is the male that offers food to its incubating or brooding partner even when both parents share parental duties. This allows the inference that, *gymnocephalus* females apparently spent twice as much time as males incubating the eggs and brooding the young.

The incubation and nestling care behaviour observed in this study agree with Brosset's (1965a) finding for *P. oreas* that incubation stints were generally not longer than 15 minutes and that the nest was not left unattended "for long". Mean interval between stints in this study was 8.2 mins and nests were left unattended for less than 4% of observed time in the incubation stage and 2.8% of observed time in the nestling stage. This probably reflected the need to guard the nest against predators (including conspecifics) and suggests that intrusion pressure increases with progress of the breeding cycle. This is supported by the fact that aggressive interactions increased from 0.087 per hour in the egg stage to 0.25 in the nestling stage and showed a significant positive correlation with nestling age (Table 3.6; Appendices 3.7 & 3.9 .).

Application of the the inclusive fitness theory to parental care implies that the duration and intensity of care represents a balance between 1) the reproductive potential of the parents on ceasing to tend the current young in favour of future broods and 2) their potential on continuing to invest further in the attempt, giving the current young a better chance of surviving to produce. One of the consequences of this theory is that willingness to provide parental care should increase through the nest cycle since it will become increasingly difficult for them to get through a replacement cycle successfully. Thus incubating eggs should be defended more vigorously than newly-laid eggs, and nestlings should be defended more intensely than eggs. The increase in aggressive interactions during the nesting cycle shown by *Picathartes* (Table 3.6) therefore provides empirical data in support of this idea.

The mating system

A key aim of this part of the study was to ascertain the type of mating system used by *Picathartes*. On the strength of a report by Brosset (1965a, b) of observations of extra birds at a *Picathartes* breeding nest, Grimes (1976) included *P. oreas* in a list of African birds which future research could show to have some degree of cooperative breeding.

The use of marked birds is essential for the elucidation of avian mating systems (Möller, 1986; Davies, 1991; Emlen, 1997). Unfortunately, although 37 *gymnocephalus* adults and nestlings were ringed in the Kambui Hills in 1992 and 1993, the premature termination of this study in the Kambui Hills (Section 2.3.2), meant that only a few marked birds were eventually observed breeding. Consequently, the picture provided of the mating system used by the birds cannot be regarded as definitive.

However, there are several indications that, at least in the breeding colonies studied here, each nest was attended by no more than a pair of birds. No more than two birds were seen attending any nest during 438 hours of observation. One of the attending birds was marked at each of four nests; two unmarked adults were not seen simultaneously at these nests (Section 3.5.3). Unmarked attending adults at these nests defended them against unmarked conspecifics. A fight was observed between a pair attending a nest and an intruding pair (Section 3.5.4.). A ringed parent provided 50% of the nestling feeds at one nest and with very few exceptions its nest visits alternated regularly with feeds by an unmarked adult (Appendix 3.10).

Tye (1987) also suggested that helpers were not present at three nests studied in southwest Cameroon, although the birds were not marked or distinguishable by plumage. Fotso (1992) did not observe more than two individuals constructing nests, incubating eggs or feeding young and notes the aggressive behaviour of nest owners to conspecifics.

The picture is far from clear however. One of the theoretical reasons for expecting cooperative breeding in a species is territory limitation or habitat saturation that limits breeding and dispersal (Komdeur, 1992; Emlen 1991, 1997). Breeding sites for *gymnocephalus* may be limited in some areas in Sierra Leone. During an intensive survey for nesting sites in the WAPF (Chapter Six), no vacant rocks were found which fitted the perceived minimal criteria as suitable nesting sites. If breeding sites are indeed limited, then a substantial non-breeding or floater population of *gymnocephalus* would be expected. There is some evidence for this. A total of 12 adult birds were banded at the Kambui Hills breeding site prior to the 1993 breeding season. A minimum of 14 birds (7 pairs) bred at this site in 1993; two of these were ringed individuals. Eight of the ringed individuals which did not breed at the site were seen there prior to and during the 1993 breeding season. Sightings of each individual ranged from 2 - 6 times over 76 days of observation. There was no evidence that these birds bred at all during the 1993 breeding season, as no other breeding site was found within a 5km radius over two years of intensive searching. These birds probably formed part of a floating, non-breeding fraction of the population.

"Floater" individuals should be expected to try to breed whenever the opportunity arises, or otherwise to maximise their inclusive fitness. Under certain conditions, several species have adopted cooperative breeding as one such strategy (Woolfenden, 1975: Perrins and Blackhead, 1983; Emlen, 1997). Alternative strategies have included breeding on alternate years or nest-robbing and infanticide (Rohwer, 1986). *Picathartes* may have opted for the latter strategy.

Breeding Success

Overall breeding success of *gymnocephalus* was 22.9% over a period of four years between 1990 and 1994. This was strikingly low compared to Grimes and Darku's (1968) results in Ghana thirty years earlier, when the percentage of eggs hatched were 100% and 82% respectively for the first and second breeding periods during three breeding seasons. Corresponding figures for the percentage of young surviving to leave the nest were 89% and 82% respectively. However, percentages of nest success were calculated using the ratio of total number of losses to the total number of eggs or

nestlings, giving final or total success for the whole nest period instead of correcting success according to the number of days exposure (Mayfield 1961, 1975). Nest content losses prior to discovery, or in this case in between nest visits do not appear in nest success calculations from this formula and results tend to be too high (Mayfield, 1961, 1975). In order to make Grimes and Darku's' (1968) results directly comparable to this study; I recalculated his results using Mayfield's method. The average survival rate of eggs was 85.4% (n = 43 eggs observed for 659 egg-days) and that of nestlings 82.9% (n = 41 eggs observed for 832.5 days). This means that the average survival rate of *gymnocephalus* through both the incubation and nestling periods in Ghana thirty years ago was 70.7%. This is still more than three times the rate observed in this study.

The reasons for this disparity are not immediately apparent. Visits to occupied nests could have increased the rate of predation and resulted in lower breeding success (Dowsett-Lemaire, 1985). However, in both Sierra Leone and Ghana, regular visits were made to occupied nests. Also, several studies have concluded that where reasonable precautions are taken there is no overall effect of nest visiting on nesting success (Brosset, 1981; Mayer-Gross *et al*, 1997). One possible explanation is that breeding success has declined over the intervening 30 years perhaps because of increased disturbance as a result of human population growth and expansion. This hypothesis can only be tested by determining the present levels of breeding success in the Ghanaian *Picathartes* population.

Data on nesting success in African forest bird species is scanty. In what is apparently the only publication in the literature on nesting success rates in African forests, Dowsett-Lemaire (1985) calculated nesting success in five forest species in the Nyika plateau in Malawi as ranging from 33% in the White-tailed Crested Flycatcher, *Elminia albonotata* to 100% in the Moustached Green Tinkerbird *Pogoniulus leucomystax*. The two species in the sample (White-tailed Crested Flycatcher and Cape Batis *Batis capensis*) which nested in open, cup-shaped nests at heights varying from 0.7 to 15m (ie nests similar to that of *Picathartes*) had success rates of 33% and 34% respectively. These success rates are closer to the rates observed in this study

(22.9%) than those obtained by Grimes (1968). Average daily mortality rates in Malawi were between 3 and 4%. This is similar to the 3.8% and 2.9% average daily mortality rates of *gymnocephalus* eggs and nestlings. These mortality rates fall within the range of daily mortality rates (1.5% - 4.5%) observed by Oniki (1979) in two equatorial forest localities in Brazil.

Mortality factors

Predation was the main cause of *gymnocephalus* nest mortality (41%). There was some evidence that snakes, monitor lizards, raptors, humans and squirrels were some of the predators responsible (Section 3.5.4).

Depredation of *gymnocephalus* nests by terrestrial predators including humans should depend on accessibility from the ground or an adjacent point of access, such as a branch or nearby rock. However, mortality rates at different nests did not vary significantly with nest height above ground (which was invariably a shorter distance than the distance to the nearest access point (Section 3.5.4). This suggests that birds were the main predators. Previous authors (Attenborough 1955, Tye 1987) have noted that depredated *Picathartes* nests were inaccessible to all but avian predators. Skutch (1950, 1985) suggested that snakes were the most important predators on nests in the tropics. This study adds to emerging evidence (eg Roper and Golstein, 1997) that this may not be the case.

Infanticide and competition from conspecifics was the second known major cause of nest losses (13.6% of the losses). Similar behaviour has been recorded by several authors in zoos (Faust 1970, McKelvey 1981, Dekker 1973) as well as in natural populations (Brosset 1965, Tye 1987). These observations and the results of this study suggest that infanticide by adult *Picathartes* is not an uncommon occurrence.

Infanticide occurs widely among different animal species and does not have a unitary explanation (Hrdy, 1979; Moller, 1988). Hrdy (1979) has categorized adaptive

explanations for infant killing as exploitation, resource competition, parental manipulation and sexual selection.

The exploitation explanation requires that the individuals responsible for an infant's death directly benefit from the consumption or use of their victim. In this study, *gymnocephalus* adults did not eat the eggs or nestlings which they removed from nests. A similar observation was made by Dekker (1973). However, McKelvey (1981) referred to *gymnocephalus* in captivity as egg-eaters and Tye (1987) suggested that adult *oreas* ate nestlings in Cameroon. The present evidence for cannibalism by *Picathartes* is therefore equivocal.

In parental manipulation, parents destroy or consume their offspring to improve their own chances of survival or that of other existing offspring (Hrdy, 1979). Belated attempts at nest defence by apparent nest owners in the cases of infanticide observed in this study, and similar observations by Attenborough (1955), Faust (1970) and Tye (1987) indicated that nest contents were destroyed by non-parent *Picathartes*. This would rule out parental manipulation as a likely explanation for nest destruction by *Picathartes*.

Hrdy (1979) recognised some infanticidal behaviour, as competition between members of one sex for reproductive investment by the other sex, which makes it advantageous for an animal (usually a male) to destroy another's offspring. Infanticide may then have two potential benefits. It may give birds direct access to limited physical resources such as food or nest sites (Rohwer 1986), or by breaking up already established pair bonds, it may give unmated birds access to mates (Rohwer 1986, Moller 1988). If the breeding season is long enough, infanticide could lead to a new breeding attempt involving the previously unmated bird (Moller, 1988). In polygynous systems, conflict over the male's parental investment is thought to be the main evolutionary force behind infanticide by females (Hansson *et al*, 1997)

If it is assumed, as the evidence from this study indicates, that *Picathartes* is monogamous, then a hypothesis explaining infanticide by *Picathartes* in terms of

competition for nests or mates would have to satisfy the following criteria:

a) there should be unmated males in a floating population;

b) nests which suffer successful infanticidal attacks should be guarded less than nests without infanticide;

c) nest sites should be limited;

d) the breeding season should be relatively long to permit renesting;

e) there should be multiple nesting attempts per season by different birds at the same nest.

There is evidence that some of these criteria obtain at *gymnocephalus* breeding sites.

Incontrovertible evidence for surplus nonbreeders in a population is usually obtained by properly controlled removal experiments (eg Bowman and Bird, 1986, Pruett-Jones and Lewis, 1990). This was not possible here because of the conservation status of the species concerned and other exigencies already mentioned (Chapter 2). However, indirect evidence for the occurrence of non-breeders at the Kambui Hills site has already been presented above (The mating system).

Dowsett-Lemaire (1985) presented evidence of nonbreeding surpluses in 21 forest species (half the forest avifauna) at Nyika in Malawi. She estimated the overall population comprised by surplus nonbreeding birds in two passerine species as 70-80% and 27-58% respectively. Nonbreeding surpluses are therefore probably not uncommon among African forest passerine species, and may well include *Picathartes.*

The presence of floaters is important in determining annual recruitment rates to the breeding population (Dowsett-Lemaire 1985). Also, Komdeur (1992) showed that disturbance by floaters lowered breeding success in the Seychelles Magpie Robin *Copsychus sechellarum*. Nest content destruction at *Picathartes* nesting sites described above (Section 3.5.4.) may have been caused by floaters.

It might be expected that infanticide would be impossible in the presence of at least one nest owner (Moller 1988, pers. obs.). Intruders within a distance of 1.5-2.0m of a *Picathartes* nest with eggs or nestlings were always attacked (Section 3.5.3). A nest

was therefore considered to be guarded if a nest owner was within about 2m of the nest. If efficient nest guarding prevents infanticide, it can then be predicted that infanticide nests would be guarded less often or less closely than nests without infanticide. The nest at which infanticide occurred in the Kambui Hills was left unattended 1.5% of 14.5 hours observation in the three days prior to the incident whilst an adjacent nest was not left unattended at all. This is a small difference; whether it is critical requires further data.

Evidence suggesting that *gymnocephalus* nesting sites may be limited has already been summarized above (Section 3.6: The mating system) and this is buttressed by the indirect indications of a substantial floater *gymnocephalus* population.

The evidence for renesting is not clear-cut. Across all study sites, most nests (16 out of 21) were used only once; but in the Kambui Hills, where two of the three cases of infanticide were observed, three of the seven nests were used more than once in 1993. The mean interval in days between successive clutches at four of the five multiple use nests recorded at all study sites was 15.3 days(range: 5-31 days, N = 12 clutches, Table 3.12). This suggests that multiple nest use was due either to the laying of replacement clutches (two cases; previous clutch failed) or nesting by a different pair (two cases; previous clutch successful). A post-fledging dependent period of 14-18 days (Dekker, 1973) means that the intervals between nesting attempts in the latter case were probably too short for double-brooding to have occurred as was reported for *gymnocephalus* in Ghana where the mean interval between nesting attempts was 127 days (Grimes 1964; Grimes and Darku 1968). Nesting by different pairs in the same nest therefore probably occurs in Sierra Leone, but at proportions which differ between sites and years.

In summary, present evidence points toward nest/mate competition at *Picathartes* breeding sites ; but with the paucity of banding data, the evidence is weak and more rigorous testing of the hypothesis would be appropriate.

Implications of observed breeding success levels for *Picathartes* population dynamics

Rare or shy species like *Picathartes* offer little possibility for precise estimation of all the parameters required for a complete description of their population demography (Clobert and Lebreton, 1991). These parameters are sex ratio, the number of eggs laid per clutch, the number of clutches per year, the number of young successfully reared to fledging per clutch, the proportion of fledged young surviving to the age of first reproduction, and the proportion of adults surviving through each age interval thereafter (Jones, 1989b; Begon, Mortimer and Thompson, 1996). Where these values are known, they can be summarized in the form of a life table that can be subjected to standard mathematical analyses (Ricklefs, 1973). Predictions can then be made about changes in the population over time.

If adequate empirical data are lacking, Clobert and Lebreton (1991) have pointed out that comparison with similar species and the exploration of theoretical or predictive models may be good ways of overcoming this difficulty . This approach is used here in an attempt to produce a framework for understanding the demography of *Picathartes* populations.

A complete life table would have age-specific, egg, nestling and fledgling survivorship entered separately. Where there is a dearth of data, the product of the mean clutch size, nestling survival, survival of fledglings to independence and the number of successful nestings per year for each age of parent females has been used as an index of age specific fecundity (m_x) i.e. the number of female eggs laid by females at different ages (Jones 1989b). Where this relationship is unknown, as in *Picathartes*, fecundity is entered as a constant for all ages (Jones 1989b).

The annual production of fledglings was calculated as 0.22 per adult from 1.92 eggs/clutch x 0.45 egg success x 0.5 nestling survival x 1 nesting of 2 adults per pair (Table 3.10). This is entered as a constant index of fecundity for all ages after the age

of first breeding in a life table for *Picathartes* (Table 3.13.). In this case, the age of first breeding is assumed to be year one. The proportion of juveniles alive at age 0 (the age at which they become independent from parental care) is taken as unity. Survival (l_x), then decreases by the juvenile survival rate until the age of first breeding and then by the adult mortality rate thereafter (Jones, 1989b; Begon, Mortimer and Thompson 1996).

Survival rates of *gymnocephalus* fledglings from independence to age of first breeding and the annual mortality rate thereafter are not known. However, several possibilities can be examined using derived values likely to have relevance for *gymnocephalus*. Data on adult mortality in African forest passerines is scanty but Dowsett (1985) provided evidence for low average annual mortalities among 17 species ranging in size from 8g to 70g. The average annual mortality rate (13.3%) of the largest species in the sample (White-chested Alethe, *Alethe fuelleborni* - 70g) would have the most relevance for *gymnocephalus* (in passerines, survival is known to increase with body size, Brooke and Birkhead 1991). Using this value (ie 87% annual survival rate), the expectation of fecundity ($l_x m_x$) each year, has been calculated assuming juvenile survival rates ranging from 50% to 75% of adult survival rates (survival of juvenile passerines is usually one-quarter to three-quarters that of adults: Ricklefs 1973) (Tables 3.13 & 3.14).

Table 3.13: Life tables for *Picathartes gymnocephalus* based on juvenile survival being (a) 50% (b) 68% and (c) 75% of an assumed annual adult survival rate of 86.7%. The mean annual fecundity is taken as 0.22 at all ages and the age of first breeding is assumed to be year one

(a) Juvenile survival = 50% of adult survival ie 0.43

Age (years)	Survival (Lx)	Fecundity (Mx)	LxMx
0	1	0	0
1	0.43	0.22	0.0946
2	0.37281	0.22	0.082018
3	0.323226	0.22	0.07111
4	0.280237	0.22	0.061652
5	0.242966	0.22	0.053452
6	0.210651	0.22	0.046343
7	0.182635	0.22	0.04018
8	0.158344	0.22	0.034836
9	0.137284	0.22	0.030203
10	0.119026	0.22	0.026186
11	0.103195	0.22	0.022703
12	0.08947	0.22	0.019683
13	0.077571	0.22	0.017066
14	0.067254	0.22	0.014796
15	0.058309	0.22	0.012828
16	0.050554	0.22	0.011122
17	0.04383	0.22	0.009643
18	0.038001	0.22	0.00836
19	0.032947	0.22	0.007248
20	0.028565	0.22	0.006284
21	0.024766	0.22	0.005448
22	0.021472	0.22	0.004724
23	0.018616	0.22	0.004096
24	0.01614	0.22	0.003551
25	0.013994	0.22	0.003079
	Ro =		0.69121

(b) Juvenile survival = 68% of adult survival ie 0.59

Age (years)	Survival (Lx)	Fecundity (Mx)	LxMx
0	1	0	0
1	0.59	0.22	0.1298
2	0.51153	0.22	0.112537
3	0.443497	0.22	0.097569
4	0.384511	0.22	0.084593
5	0.333371	0.22	0.073342
6	0.289033	0.22	0.063587
7	0.250592	0.22	0.05513
8	0.217263	0.22	0.047798
9	0.188367	0.22	0.041441
10	0.163314	0.22	0.035929
11	0.141593	0.22	0.031151
12	0.122761	0.22	0.027008
13	0.106434	0.22	0.023416
14	0.092278	0.22	0.020301
15	0.080005	0.22	0.017601
16	0.069365	0.22	0.01526
17	0.060139	0.22	0.013231
18	0.052141	0.22	0.011471
19	0.045206	0.22	0.009945
20	0.039194	0.22	0.008623
21	0.033981	0.22	0.007476
22	0.029461	0.22	0.006482
23	0.025543	0.22	0.005619
24	0.022146	0.22	0.004872
25	0.0192	0.22	0.004224
	Ro =		0.948404

Table 3.13 (cont): Life tables for *Picathartes gymnocephalus* based on juvenile survival being (a) 50% (b) 68% and (c) 75% of an assumed annual adult survival rate of 86.7%. The mean annual fecundity is taken as 0.22 at all ages and the age of first breeding is assumed to be year one

(c) Juvenile survival = 75% of adult survival ie 0.65

Age (years)	Survival (Lx)	Fecundity (Mx)	LxMx
0	1	0	0
1	0.65	0.22	0.143
2	0.56355	0.22	0.123981
3	0.488598	0.22	0.107492
4	0.423614	0.22	0.093195
5	0.367274	0.22	0.0808
6	0.318426	0.22	0.070054
7	0.276076	0.22	0.060737
8	0.239357	0.22	0.052659
9	0.207523	0.22	0.045655
10	0.179922	0.22	0.039583
11	0.155993	0.22	0.034318
12	0.135246	0.22	0.029754
13	0.117258	0.22	0.025797
14	0.101663	0.22	0.022366
15	0.088142	0.22	0.019391
16	0.076419	0.22	0.016812
17	0.066255	0.22	0.014576
18	0.057443	0.22	0.012637
19	0.049803	0.22	0.010957
20	0.043179	0.22	0.009499
21	0.037437	0.22	0.008236
22	0.032457	0.22	0.007141
23	0.028141	0.22	0.006191
24	0.024398	0.22	0.005368
25	0.021153	0.22	0.004654
		Ro =	1.044852

Table 3.14. Net reproductive rate (R_o) of Picathartes at different juvenile survival rates

Assumed Life Span (years)	Total expected fecundity ($\sum l_x m_x = R_o$) at different annual juvenile survival rates: 43%	59%	65%
25	0.69	0.94	1.04

The total expectation of fecundity during a female's entire life span (the sum of $l_x m_x$) is referred to as R_o, the net reproductive rate. A value of less than 1.0 for R_o means that each female will not replace herself during her lifetime and that the population will therefore decline, whereas a value greater than 1.0 indicates an increasing population (Jones 1989b). Table 3.13 & 3.14 show that, assuming 86.7% annual adult survival, very few adults live as long as 25 years and that annual juvenile survival rates of 65% or more (ie more than 75% of the annual adult survival rate) would be required for *Picathartes* populations to stabilize over this 25 year life span.

There are several indications that the values used in the above model are conservative. The adult annual survival rate used in the model (86.7%) was the highest recorded for the 17 African forest species studied in Malawi (Dowsett 1985) and also higher than the rates recorded for a variety of non- forest species from Africa (Fry 1980, Oatley 1982). Only 5% of northern and southern temperate passerine species have survival rates greater than 80% (Rowley and Russell, 1991) and in the neotropics, survival rates greater than 85% occur in less than 10% of studied species (Bell 1982, Skutch 1985). Secondly, the model has assumed that age of first breeding for *Picathartes* is at one year. This is unlikely if nesting sites are limited and survival of adult breeders is high (adult survival of more than 80% has been assumed). Finally, the primary productivity figure used as an index of fecundity is probably higher than what obtains

in the natural population, as the possible effect of a nonbreeding surplus has not been taken into account (Dowsett-Lemaire 1985).

In conclusion, *Picathartes* probably conforms to the pattern of low reproductive rate, long life and delayed sexual maturity typical of tropical passerines (Fogden 1972, Diamond 1974). However, unless *Picathartes* juvenile survival rates are higher than the averages hitherto known to occur in other tropical forest species (Fry 1980, Skutch 1985, Dowsett 1985, Rowley and Russell 1991), the low primary productivity of *Picathartes* populations in Sierra Leone suggest that these populations are almost certainly declining.

CHAPTER FOUR

THE ANNUAL CYCLE IN RELATION TO SEASONALITY OF ENVIRONMENTAL FACTORS.

4.1. AIMS

This chapter has two main aims:

1. To examine how two key environmental resources - food and rainfall - changed with season in the vicinity of *Picathartes gymnocephalus* breeding sites.
2. To investigate the relationship between the main events in the annual cycle of *gymnocephalus* (moult and breeding) and the variation in environmental factors.

4.2. PREVIOUS WORK

4.2.1. Timing of breeding

Previous work concerning the annual cycle of *Picathartes* has focussed on determining when the birds breed in relation to rainfall patterns. There has not been any previous attempt to measure food abundance or relate this to the breeding cycle.

Grimes and co-workers (1963, 1964, 1968) carried out the only previous systematic study of breeding in *Picathartes gymnocephalus* by regularly inspecting 5 - 6 nests at a single site in Ghana over a period of three years. The results suggested two breeding periods, one from March to June, the other from September to November, with breeding periods coinciding with the two peaks of the bimodal rainfall pattern in the area.

Less systematic information from Sierra Leone presented an unclear picture. According to Glanville (1954), breeding takes place from April to October in

association with the single wet season. A former Chief Conservator of Forests in Sierra Leone - J.S. Sawyerr (1965, *in litt* to L.Grimes) suggested that eggs were laid twice a year, from February to May (during the dry season) and September to December (mainly in the wet season). Allport *et al* (1989) found four nests, each with two eggs, in November, December, January and February in the Gola forest area.

In Liberia, Colston and Curry-Lindahl (1986) found *gymnocephalus* nestlings, in mid-dry season on Mount Nimba in Liberia.

For *P. oreas*, there are numerous records of eggs and nestlings from different areas at different times of the year (see Collar and Stuart, 1985), but systematic site-specific studies extending across more than one season are few. Brosset (1965a) found that breeding of *oreas* in northeast Gabon, occurred between March and May in two successive years (the wet season is from October to May). Serle (1981) showed that *oreas* was a wet season breeder at Mamfe in west Cameroon, with all records of nests with eggs or nestlings (15) falling between May to October. But Tye (1987) recorded *oreas* breeding in December and January (the dry season) at 700m on the southwest slopes of Mount Cameroon (n=6 nests). Ash (1991) found *oreas* nests (n=26) with eggs and nestlings between September and October (during the wet season) in southeastern Nigeria in 1987. Fotso (1993) observed 17 egg-layings at 28 occupied nests in southern Cameroon over nine months and found that eggs were laid from March to November with peaks in June/July and October. This period corresponds with the wet season in Southern Cameroon (April to November)(Fotso 1992).

4.2.2. Moult

There has not been any previous work on the moult of *Picathartes gymnocephalus*. Brosset (1965a) inferred from the appearance of *P. oreas* rectrices and remiges at a distance and the many feathers found on the floor of a roosting cave that *oreas* in northeast Gabon moulted in July - August, the driest months of the year. There is no previous information on the pattern and duration of moult in *Picathartes*.

4.3. METHODS

Field observations of adult *Picathartes* (Section 3.4.) showed that prey were almost always captured either on the forest floor or on surfaces not exceeding 0.5m in height. Therefore, to assess how the timing of *Picathartes* breeding and moult related to any changes in food abundance levels, I measured variations in the abundance, diversity and biomass of ground level organisms.

4.3.1. Feasibility studies

Three methods were used to measure ground-storey fauna abundance: pitfall traps, malaise traps, and visual censuses. These methods (apart from malaise traps) were chosen after an evaluation of several methods during feasibility studies in 1990 (malaise traps were acquired in 1992 and used without any prior trials).

The feasibility studies were carried out between June and December in the Gola Forest and WAPF and evaluated six methods of sampling ground-story fauna: pitfall traps, litter sampling, visual surveys, water traps, sweep netting and sticky traps. These methods were selected from the range of sampling methods available for surveying ground-storey fauna (see Sutherland, 1996 for recent review), on the basis of availability and cost.

Six pitfall traps were set up along a 40m stretch of path, about 100 -200m from a *gymnocephalus* breeding colony in each forest. Trap positions were located as described below (Section 4.3.2) and traps allowed to operate for two weeks before being emptied. Two sticky traps (yellow, single-sided adhesive surfaces: 10cm x 20cm) and a water trap (a white tray - 15cm diameter and 1 cm deep) were erected close to each pitfall trap so that a total of twelve sticky traps and six water traps were positioned close to each colony, about 0.5m above ground. These traps were also allowed to operate for two weeks. The path was walked very slowly, once a week and the numbers and types of all organisms seen directly in front of the observer recorded. Fourteen litter samples were collected at random along the path from within 0.5m x

0.5m quadrats at the end of the trial period. A muslin sweep net (18 cm diameter aperture) mounted on a 1.5m wooden handle was used to trap organisms at 5m intervals along the transect once a week.

Trapping of ground-storey fauna was accompanied by 93 hours of direct observations of adult *gymnocephalus* feeding nestlings at both colonies (Section 3.4.2.).

All trapped organisms were treated as described below (Section 4.3.2) and preliminary analysis carried out to get an idea of the numbers, types and sizes of organisms being trapped.

Final selection of the methods used in the study was based on their effectiveness at trapping organisms that were likely to be prey items for *Picathartes* and the time and effort for implementation. On these criteria, it was decided not to use water traps and sticky traps. Water traps caught the lowest numbers of organisms of all the methods tested and were clearly ineffective. The majority of the invertebrates caught by sticky traps were regarded as too small to serve as potential prey for *Picathartes*.

Sweep net sampling and litter sampling were initiated in the Gola forest and Kambui Hills but discontinued because of lack of time to carry them out during site visits.

4.3.2. Sampling methods

Undergrowth fauna were monitored in the Kambui Hills from June 1992 to November 1993. Trapping was initiated in the Gola forest in December 1992 but discontinued after five months because regular visits to the study site were no longer possible.

Pitfall trapping

Pitfall traps were set up in forest habitat 40m east of the study colony in the Kambui Hills and in the centre of a patch of farmbush (about 1.5 ha in size and two to three years old) 200m to the southwest of the colony.

In both forest and farmbush, ten pitfall traps were randomly positioned in a 100m x 100m grid set up along a 100m base line. Trap positions were determined by selecting random "coordinates" (lucky dip method) which represented sampling points at varying distances along and away from the base line. Random numbers were in multiples of ten, to ensure 10m separation between traps. Each pitfall trap was a 737 cm^3 tin, dug into and level with the soil surface. Each tin had an aperture diameter of 85mm, making a total trapping area for ten traps at each site of 568 cm^2. Holes were punched close to the top of each can, to reduce the chances of flooding during rainfall. The trap liquid used was 70% alcohol (it was the most easily obtainable) which occupied about one-third of the tin's capacity. In the dry season, this was increased to about half the tin's capacity to compensate for evaporation.

Traps were emptied once every two weeks whenever possible.The contents of each trap were examined separately and the organisms classified as far as possible. Individual trap contents were weighed, air-dried for two to three days, then re-weighed. All organisms collected from the ten traps in the same grid for the same data period were then stored in the same appropriately labelled container.

Malaise traps

A malaise trap is an interceptive device made of fine-meshed netting that uses a series of baffles to funnel flying and leaping insects into a closed and removable chamber, that in this study, contained 70% alcohol. One trap was set up in forest about 20 m away from the Kambui Hills breeding site in September 1992 and operated continuously till May 1993. The trap was emptied once every fortnight whenever possible and the contents treated in a similar manner as those of pitfall traps.

Visual surveys

A 1.2 km rectangular transect which started and ended at the breeding colony in the Kambui Hills was walked slowly twice each month on successive days so that each

walk lasted about 90 minutes. All organisms detected in a band 0.5m wide and up to 0.5m high on the path directly in front of the investigator were identified (usually to the level of order), counted, and the data recorded. An effort was made to do each walk at around the same time of the day (mid-morning) and in fine weather. Visual surveys were carried out from December 1992 to November 1993 but were suspended at the height of the wet season (June - August) because of rain.

Rainfall

In the WAPF, rainfall data were compiled from the records of a local water company (Guma Valley Water Company) which had rain gauges in the forest within the study area.

In the Kambui Hills and the Gola forest, rainfall data were obtained from meteorological stations located in nearby main towns. In the case of the Kambui Hills, data were used from Bo (45 km away) and for Gola from Daru (25 km away). Although, the magnitude of rainfall within the forest will be different from that outside, the patterns of temporal variation (which were required here) are generally quite similar within the same region of the country (see Chapter 2).

4.3.2. Monitoring events in the annual cycle

The timing of breeding

Data on the timing of breeding were obtained from regular nest inspections (Section 3.4.2) during which the numbers of eggs and nestlings found in nests were recorded.

Moult

Wing moult was recorded when adult birds were trapped (Section 3.4.3.). Primary moult was scored after Ashmole (1962), from zero for old feather to 5 for a new one. Nine primaries were scored (the tenth is much shorter than the rest), birds were

therefore given a score of 90 when all primaries were fully grown and fresh. Moult of the secondaries (six) were recorded in the same way

4.4. RESULTS

4.4.1. Environmental factors

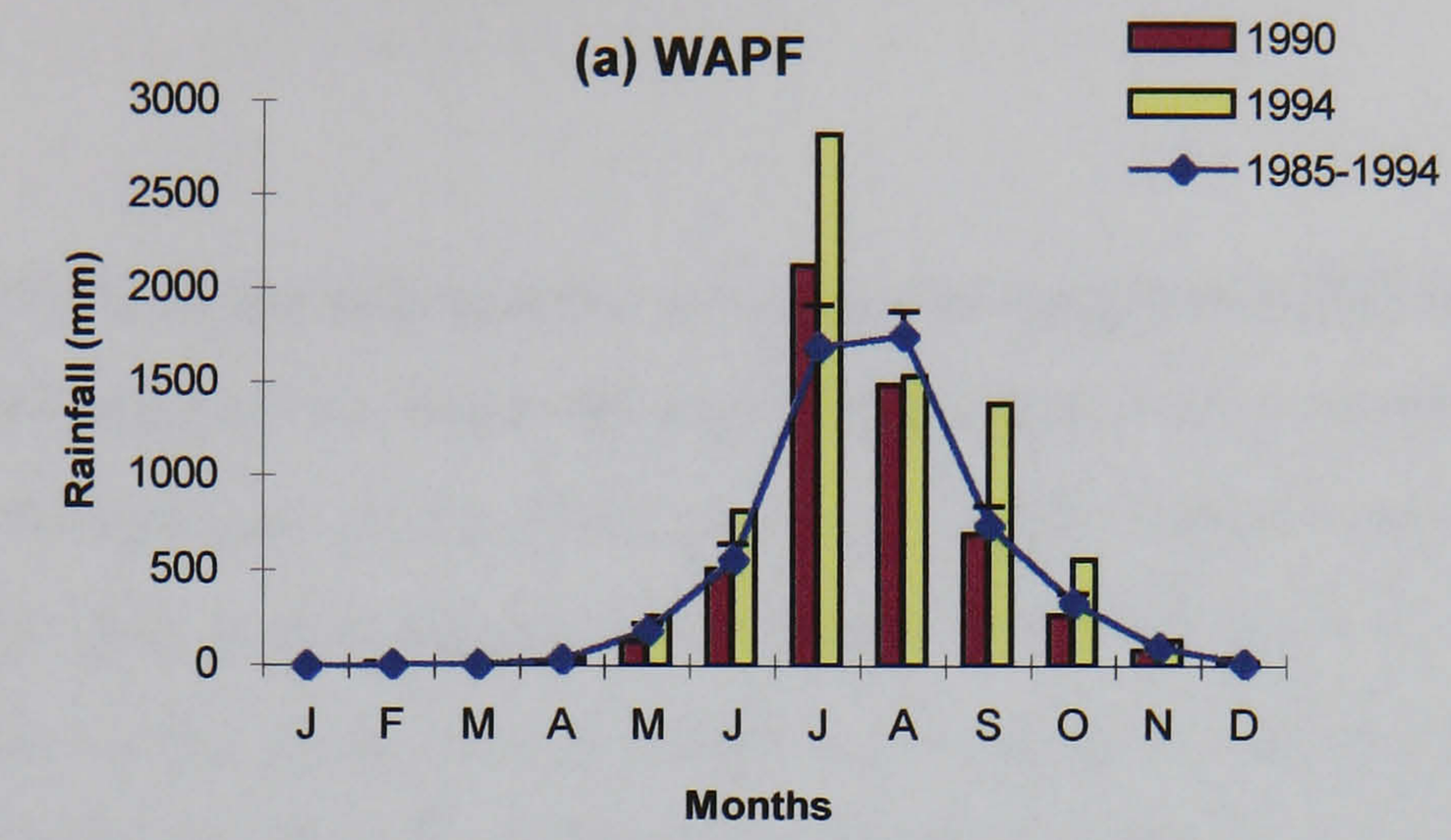
Rainfall

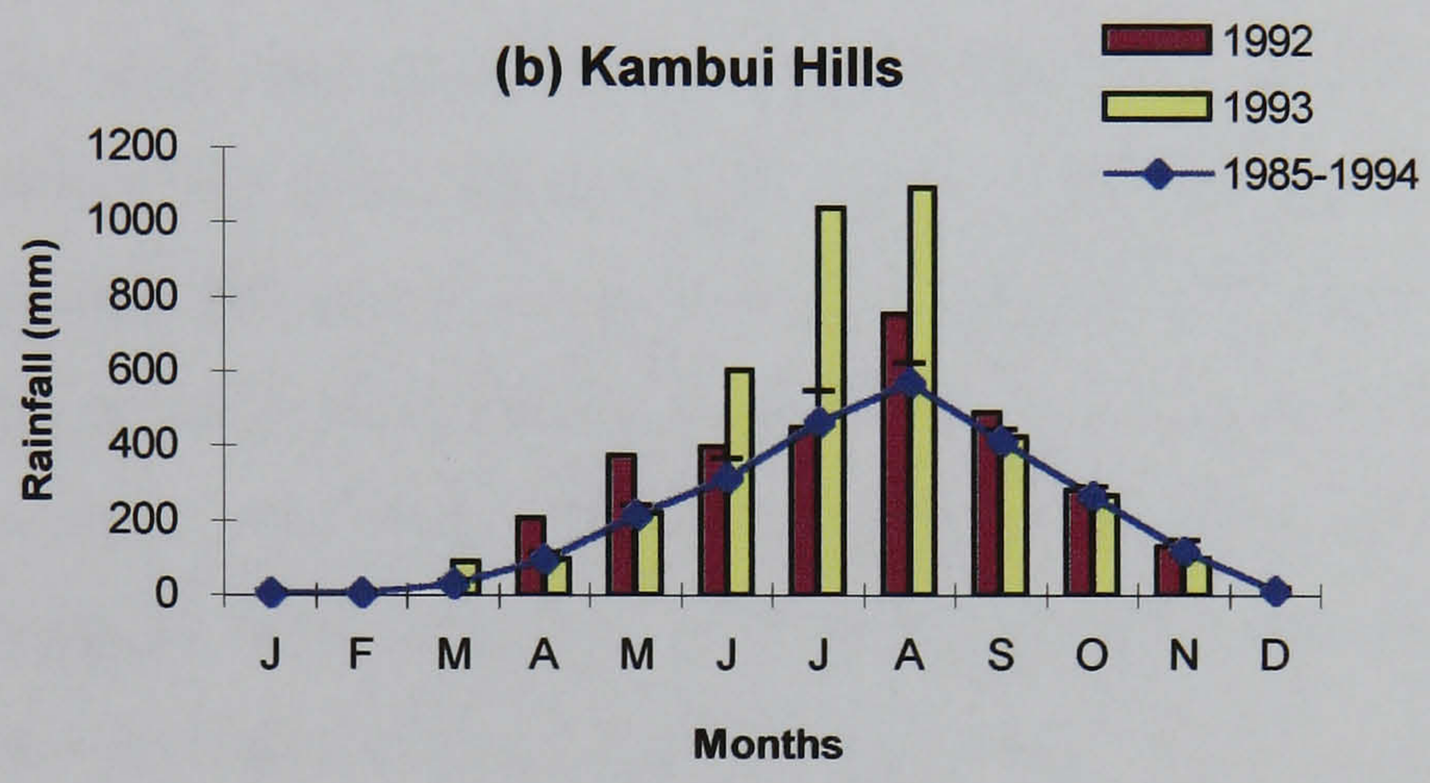
Rainfall seasonality was similar in all three study areas with peak rainfall in July and August (Fig 4.1). However, in the east of the country (Kambui Hills and Gola Forest areas), the wet season was more prolonged than in the WAPF. On average, rain fell for only seven months of the year (May to November) in the WAPF (Figs. 4.1a and 4.1d) whilst in the east only January regularly did not have any rainfall. Also, mean annual rainfall in the WAPF (5385.2 ±353 mm, n = 10 years), was significantly higher ($F_2 = 50.8$; $p < 0.001$) than that in the region of the Kambui Hills (2579.1±231.1mm, n = 8years) and the Gola Forest (2215±46.4 mm, n = 11 years) respectively (Fig.4.1d & Appendix 4.1).

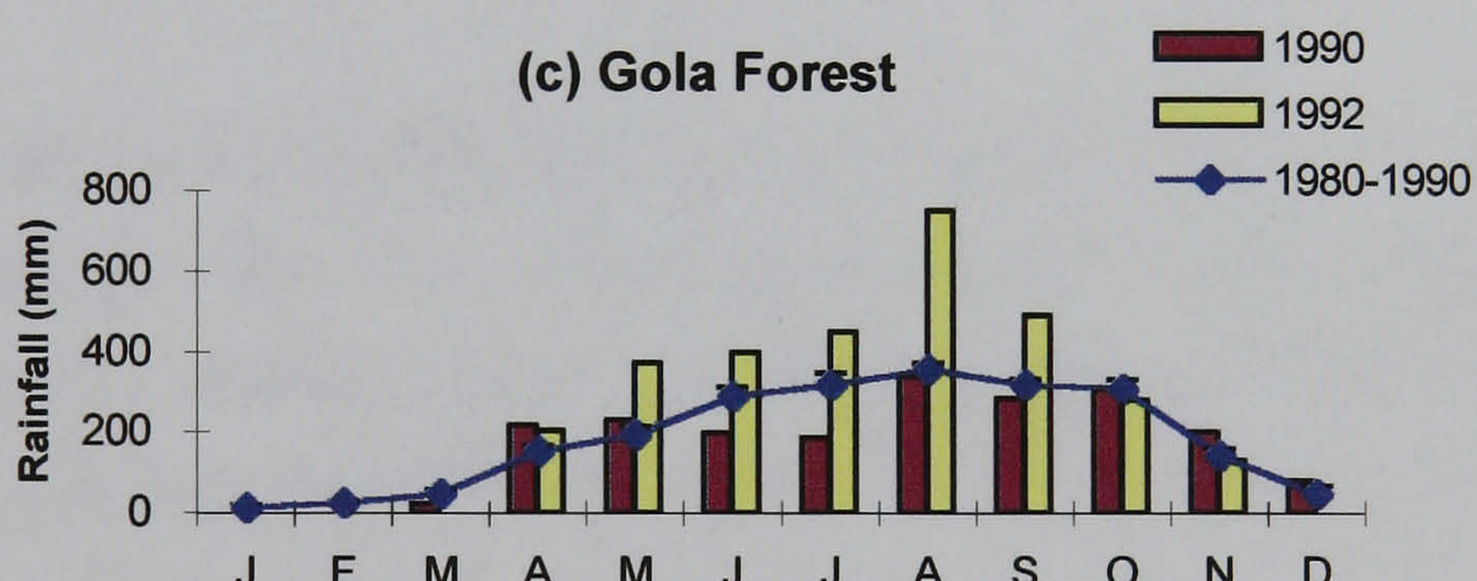
In 1990, monthly rainfall was lower than average in the WAPF (Fig.4.1a.) and the Gola forest (Fig. 4.1c). for most of the wet season. Conversely, monthly rainfall levels were higher than average in the Gola forest region in 1992 (Fig. 4.1c).and in the WAPF in 1994 (August being an exception)(Fig.4.1a.)

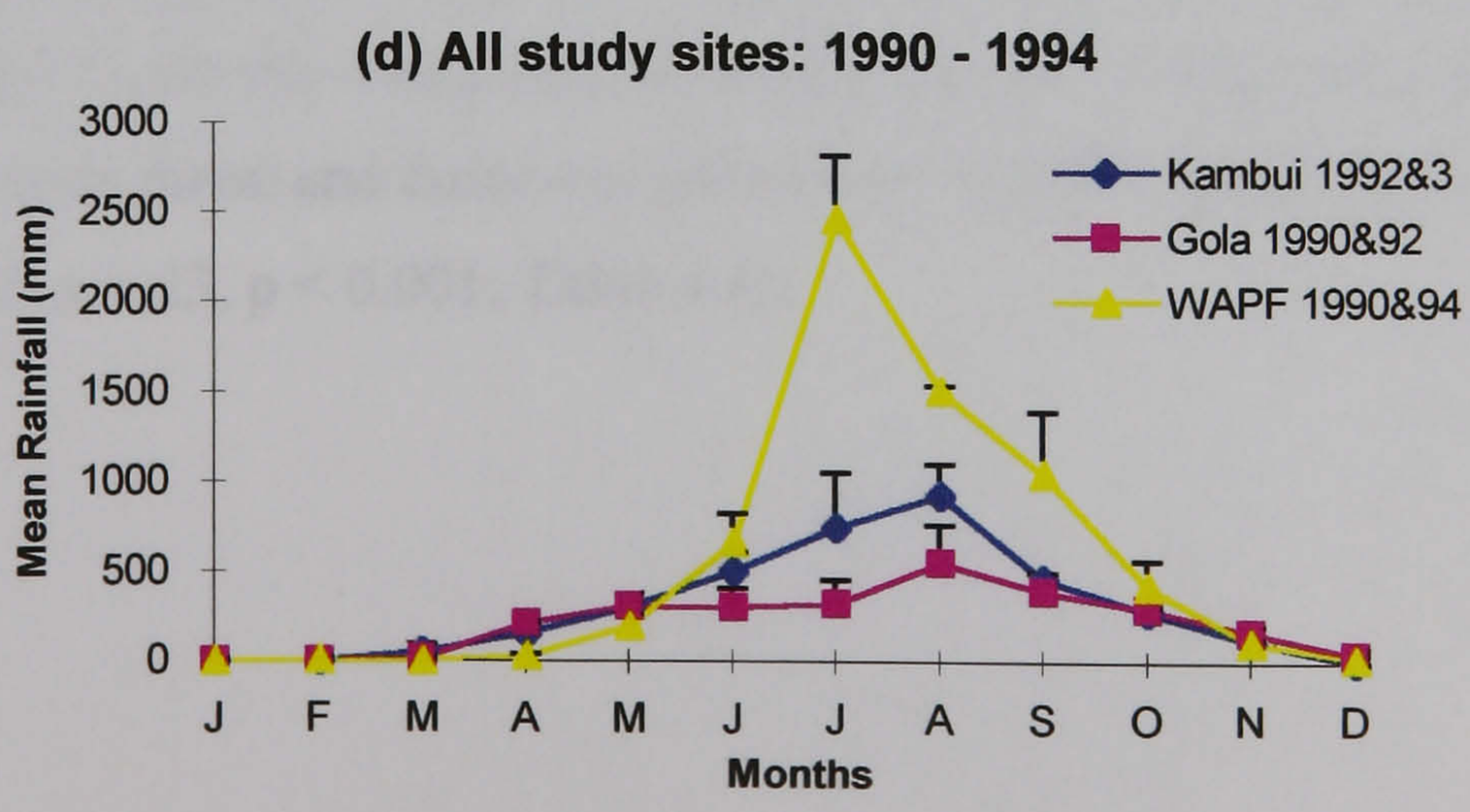
Monthly rainfall levels in the Kambui Hills were close to or just above average levels during the study period (1992 and 1993), except that in 1993, rainfall at the peak of the wet season (June - August) was higher than average (Fig. 4.1b).

Fig. 4.1. Mean and actual monthly rainfall (mm) at study sites









Composition and density of fauna

Pitfall traps

Arthropods represented 94% of the total number of organisms caught in pitfall traps in the Kambui Hills in 1993, the year for which the most complete records were obtained (Table 4.1.). Of the 3445 organisms greater than 3.0 mm in length caught in samples (n = 240), Formicidae (22.8%; mainly Myrmicinae), Coleoptera (21.6%; mainly Byrrhidae), and Isoptera (15.2%; mainly Rhinotermitidae) were the most abundant groups; together constituting almost 60% of the total numbers (Table 4.1). Culicine mosquito larvae (12.1%); other insect groups (8.4%), and unidentified larvae (5.8%) accounted for another 26% of the total numbers. Gastropoda (Pulmonata and Prosobranchia), Oligochaetae, Mosquito pupae (mainly culicines), Orthoptera, Diplopoda and Araneidae each constituted between 3% and 1% of the total number of organisms trapped. Each of the remaining 15 groups comprised less than 1% of the total numbers caught (Table 4.1 & Appendix 4.2). Mosquito larvae and pupae were probably laid in the traps and were not caught by the traps per se.

Mean numbers per sample (±s.e.) of different animal taxa which occurred in forest and farmbush pitfall traps and their relative abundance (percent) in the two habitats are also shown in Table 4.1. Coleoptera formed the largest proportion (33.4%) of individuals caught in the forest samples followed by Formicidae (17.9%) and Isoptera (15.7%). In farmbush habitat, Formicidae predominated in the samples (27.2%). Culicine larvae (20.8%), Isoptera (14.7%) and Coleoptera (11.0%) were the next most abundant taxa (Table 4.1). On the whole however, there was good agreement in rank order correlation between forest and farmbush pitfall trap catches (Spearman's rank correlation, $r_s = 0.742$, $n = 23$, $p < 0.001$; Table 4.1).

Table 4.1. Mean numbers per sample (± s.e.) and relative abundance (%) of organisms in pitfall trap samples in forest (n=133) and farmbush (n=107) in the Kambui Hills - 1993. Asterisks indicate significant differences in mean numbers per sample between forest and farmbush.

Taxonomic group	Mean nos per sample		Relative abundance(%)		Overall percent
	nos in forest	nos in farmbush	% in forest	% in farmbush	(of total caught)
Apidae	0.06±0.036	0.02±0.013	0.43	0.11	0.26(9)
Araneidae	0.24±0.054	0.14±0.045	1.78	0.88	1.31(45)
Bufonidae	0.17±0.043	0.12±0.045	1.23	0.66	0.93(32)
Chilopoda*	0.02±0.013	0.15±0.039	0.18	0.82	0.52(18)
Coleoptera*	3.88±0.773	1.8±0.259	33.4	11.0	20.1(745)
Culicine larvae	0.16±0.078	3.74±3.04	1.23	20.8	12.1(416)
Culicine pupae	0.14±0.067	0.37±0.388	1.04	2.5	1.80(62)
Culicidae	0.14±0.097	0.04±0.037	1.04	0.22	0.61(21)
Dictyoptera	0.05±0.019	0.0	0.31	0	0.15(5)
Diplopoda	0.16±0.035	0.22±0.054	1.17	1.3.	1.28(44)
Diptera	0.02±0.013	0.01±0.009	0.18	0.06	0.12(4)
Formicidae*	2.24±0.294	4.61±0.759	17.9	27.2	22.8(784)
Gastropoda*	0.52±0.078	0.21±0.049	3.92	1.28	2.53(87)
Hemiptera	0.03±0.025	0.01±0.009	0.25	0.06	0.15(5)
Isopoda	0.0	0.02±0.017	0	0.17	0.09(3)
Isoptera	2.01±0.468	2.47±1.043	15.7	14.7	15.2(522)
Oligochaetae	0.38±0.072	0.35±0.073	2.94	1.87	2.55(85)
Orthoptera	0.1±0.037	0.31±0.155	0.8	1.76	1.31(45)
Other Insect groups+	0.99±0.156	1.09±0.442	7.79	8.87	8.36(288)
Unid. arthropods	0.01±0.008	0.0	0.06	0.11	0.09(3)
Unid. pupae	0.16±0.098	0.0	1.17	0.0	0.55(19)
Unid. larvae	0.94±0.149	0.748±0.187	7.3	4.4	5.76(199)
Vespoidea	0.02±0.017	0.0	0.18	0.0	0.09(3)

+Includes Dermaptera

Formicidae and Chilopoda occurred in farmbush samples in numbers that were significantly greater than those trapped in forest (t test: t = -2.9 and -3.029 respectively, $p < 0.005$ and n = 240 in both cases; Table 4.1). Conversely, Coleoptera and Gastropoda occurred in statistically significant greater numbers in forest samples than in farmbush samples ($t = 2.554$, $p < 0.005$ and $t = 3.433$, $p < 0.001$ respectively; n = 240 in both cases). Differences between numbers of all other groups were not statistically significant (Table 4.1).

Total pitfall trap catches (numbers and biomass) over the whole year were higher in farmbush habitat than in forest but the differences were not statistically significant (Table 4.2; $t_{125} = -1.256$, $p > 0.2$, n = 240 and $t_{14} = -1.338$, $p > 0.2$, n = 30 respectively)(numbers of sampling units differ because different numbers of traps were flooded or otherwise became inoperative in the two habitats).

Table 4.2. Mean numbers and dry weight (mg) of organisms trapped by pitfall traps in forest and farmbush in the Kambui Hills in 1993.

	Forest	Farmbush
Mean nos per trap ±se (n)	12.3 ±1.08 (133)	16.9 ±3.6 (107)
Mean dry weight (mg) per trap period(se (n)	5.4±1.7 (17)	12.1±3.6 (13)

Malaise traps and visual surveys

The proportions of different animal taxa seen during visual surveys and which occurred in malaise trap samples in the Kambui Hills (forest habitat) are shown in Table. 4.3. The results for the visual surveys refer only to animals which occurred solitarily or in small groups. Organisms which occurred in clumps and could not be

counted individually (termites and army ants) are excluded from the following analysis and are dealt with separately below.

Araneidae (32.3%) and Formicidae(23.4%) occurred most frequently on visual surveys (Table. 4.3). Unidentified pterygotes (the majority of which were almost certainly Diptera)(17.7%), positively identified Diptera (7.6%) and Orthoptera (4.9%) comprised another 30% of total numbers. Five taxa (Hemiptera, Dictyoptera, Odonata, Diplopoda and Anura) each formed 1-2% of the census total. The numbers of each of all other groups constituted less than 1% of the total.

The bulk of the malaise trap catch comprised winged Hymenoptera (34.3%), Diptera (19.5%) and Lepidoptera (16.9%). Coleoptera (8.8%), Orthoptera (2.4%) and Odonata/Ephemeroptera (1.5%) were the only other taxa recorded in numbers greater than 1% of the total)(Table 4.3).

Comparison of the different sampling methods

Pitfall trap samples and visual surveys were closely matched in rank order abundance across taxa ($r_s = 0.592$, $p < 0.001$) whilst the composition of malaise trap samples showed little or no rank order correlation with either pitfall trap samples or visual surveys (r_s =0.047 and 0.117; $p > 0.5$ in both cases)(Tables 4.1 & 4.3).

Table 4.3. Proportions of different animal groups in malaise trap samples and visual surveys in the Kambui Hills. Taxa arranged in descending order of abundance.

Taxa	Percentage of total numbers	
	Visual surveys	Malaise trap
Araneidae	32.35	1.64
Formicidae	23.4	0
Unid Pterygotes	17.1	12.5
Diptera	7.62	19.46
Orthoptera	6.94	2.44
Hemiptera	2.31	0.71
Dictyoptera	1.99	0.57
Odonata	1.95	1.67
Diplopoda	1.34	0
Anura	1.18	0
Cicadidae	1.06	0
Gastropoda	0.61	0
Lacertilia	0.81	0
Unid Apterygotes	0.37	0
Apidae	0.21	0
Chilopoda	0.12	0
Caterpillars	0.08	0
Thysanura	0.08	0
Coleoptera	0.08	8.81
Oligochaetae	0.08	0
Psocoptera	0.04	0.03
Hymenoptera	0.04	34.29
Hirudinea	0.04	0
Ephemeroptera	0	0.13
Homoptera	0	0.096
Isopoda	0	0.06
Dermaptera	0	0.32
Trichoptera	0	0.032
Lepidoptera	0	16.89
Thysanoptera	0	0.16
Mecoptera	0	0.03
Isoptera*	na	0.32

*na = not applicable

Seasonality of fauna

Pitfall traps

Catch per unit effort in forest habitat (where the most complete records were obtained) was markedly higher at the end of the rains in late November and in December 1992 than in the preceding four months of the wet season. This was more clear-cut for biomass than numbers (Fig 4.2). Biomass catch levels remained significantly elevated in January and February 1993 but did not show any clearly defined seasonal variation for the rest of the year. However, there were minor but distinct peaks in numbers trapped in late May and in early July and early August 1993, repeating to some extent a weak trend in 1992 (peaks in early June and August; Fig 4.2).

The pattern of variations in numbers of organisms captured in pitfall traps at different times of the year was similar in forest and farmbush habitat ($r_s = 0.778$, $n = 14$, $p < 0.002$) with decreased catch levels toward the latter half of both the dry (Feb - Mar) and wet seasons (Sep-Oct) (Fig 4.3)

There was significant negative correlation between fluctuations in the biomass of pitfall trap samples and rainfall seasonality but correlation between seasonality and pitfall sample numbers was not significant (Table 4.4).

Peaks in forest pitfall trap catches in August and November-December 1992 were due mainly to large numbers of termites in the samples (Figs 4.2 & 4.6a). In mid-December 1992, small insects (< 3mm in length) which could not be identified with any certainty formed a large proportion of the catch and contributed substantially to the peak in numbers observed at this time (Appendix 4.2). This is probably the reason for the discrepancy between numbers (relatively high) and biomass (relatively low) observed in mid-December (Fig 4.2).

Increased abundance of Coleoptera in forest pitfall trap samples was mainly responsible for the elevated biomass levels observed in January and February 1993

compared to the rest of the year (Figs 4.2 & 4.6a). Also minor peaks in catch levels in May and July coincided with increased occurrence of Coleoptera in pitfall trap samples.

In farmbush, peaks in the abundance of the three major taxa in the samples - Formicidae, Coleoptera and Isoptera coincided with increased catch levels in May and July/August. Peaks in numbers of Isoptera tended to occur slightly ahead of increases in the numbers of Formicidae and Coleoptera. (Figs 4.3 & 4.6b).

Table 4.4. Spearman rank correlations between monthly rainfall and abundance of undergrowth fauna monitored by different methods in the Kambui Hills Forest: 1992-1993.

Monitoring Method	Correlation	N (months)
Pitfall trap sample biomass	- 0.597**	17
Pitfall trap sample numbers	- 0.336	17
Malaise trap catch biomass	- 0.178	14
Malaise trap numbers	- 0.538*	14
Visual census numbers	- 0.226	9
Numbers of ant columns	- 0.485	9
Numbers of termite columns	0.274	9

*P < 0.05, **P < 0.02.

Malaise traps

Malaise trap catch numbers did not fluctuate in any definite seasonal pattern (Fig 4.4) but variation in the biomass of the catches was negatively correlated with rainfall ($p < 0.05$; Table 4.4).

Variations in the numbers of the major groups in malaise trap samples (Diptera, Lepidoptera and Hymenoptera) mirrored changes in overall catch levels from

February to October 1993 (Figs 4.4 & 4.6c). However, changes in overall catch levels between September 1992 and February 1993 are not reflected in catch rates of these main groups . The overall changes (a peak in numbers and biomass in November and a peak in biomass in January) probably reflected increased abundance of Coleoptera and small (<3mm length) insects which occurred in the malaise trap catches at this time (Appendix 4.4).

Visual surveys

The numbers of animals seen on visual surveys were not significantly correlated with monthly rainfall ($p > 0.5$, Table 4.4.). However some signs of the weak trends shown by pitfall trap catches were also detectable in visual surveys. Numbers recorded in the latter half of the dry season (Feb-Mar) and the wet season (Sep-Oct) were lower than at other times (Fig 4.5).

Visual census results clearly reflected changes in the numbers of Araneidae and Formicidae seen (Fig 4.5.& 4.6d).

The occurrence of army ant columns and termite concentrations in visual censuses were not significantly correlated with rainfall seasonality (Table 4.4) but there was a clear pattern to the variation in the numbers seen (Fig. 4.6d). Numbers were highest in February and declined in the latter half of the dry season (March - April). Numbers were relatively low during the wet season but showed signs of increasing at the start of the dry season (November) (Figs 4.5. & 4.6d). It must be noted however that censuses were not carried out in the middle of the wet season.

In summary, all three sampling methods used showed increased levels of faunal abundance at the onset of the wet season ie May (exception- ant columns and termite concentrations). Numbers were relatively low in the wet season, showed peaks at some point in the early dry season between November and February and tended to decline again in the latter part of the dry season. However, it should be noted that delays between rainfall and responses of the undergrowth fauna might have obscured the effects.

Fig 4.2. Numbers and biomass (mg) of organisms caught in forest pitfall traps: Kambui Hills 1992-1993

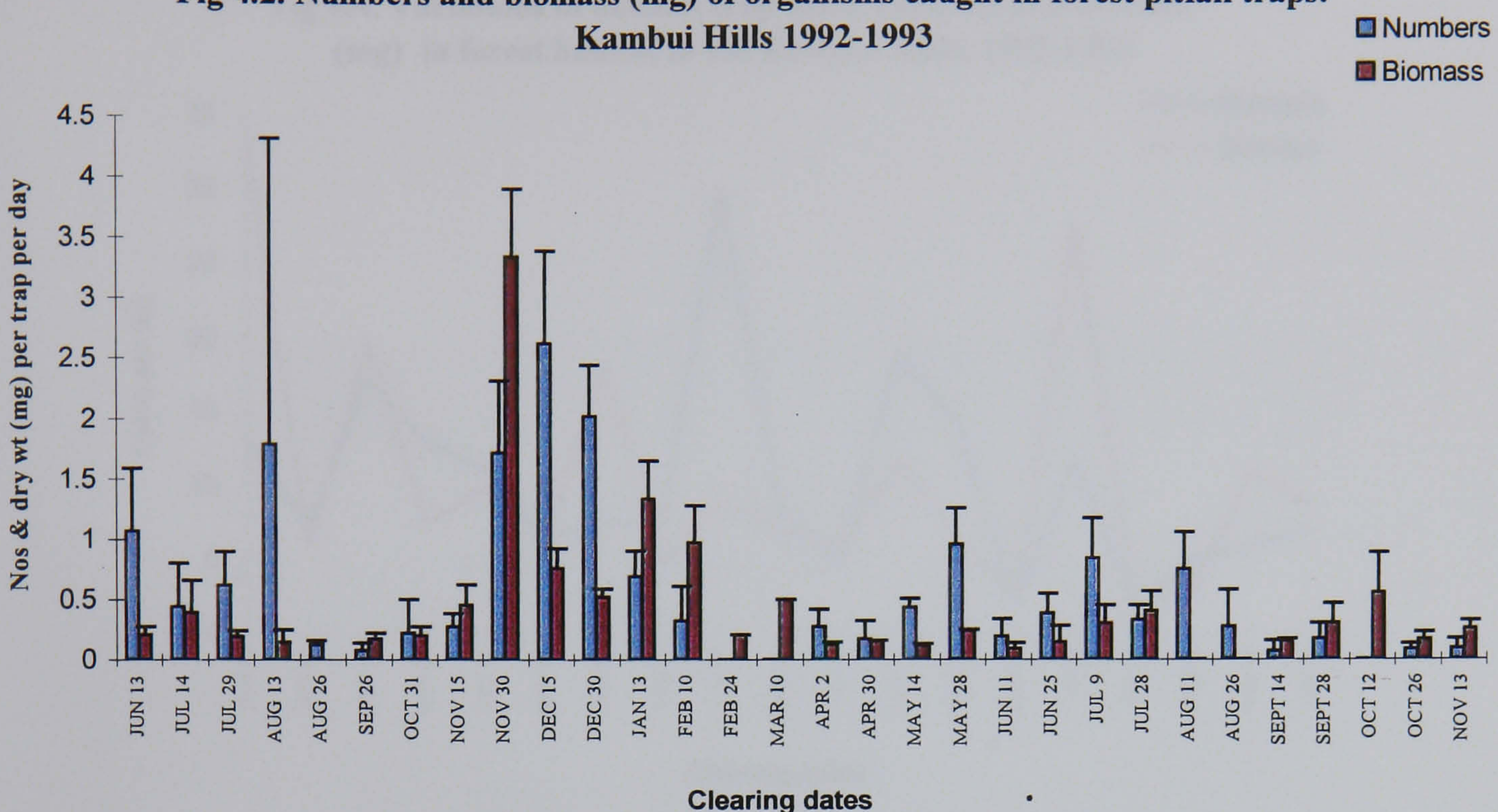


Fig 4.3. Comparison of the variation in the numbers of organisms caught in forest and farmbush pitfall traps: Kambui Hills 1993

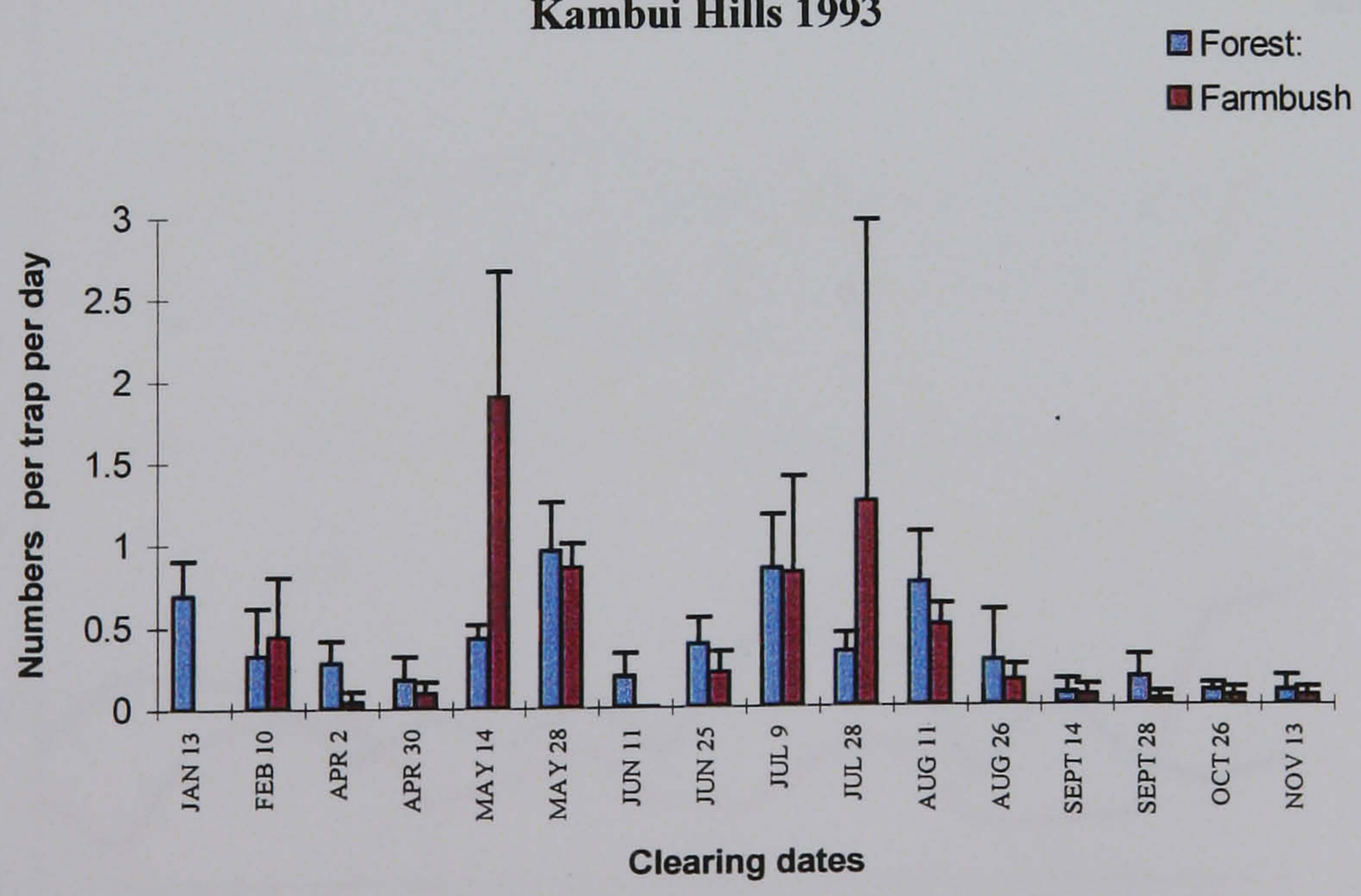


Fig 4.4. Variations in malaise trap catch numbers and biomass (mg) in forest habitat in the Kambui Hills: 1992-1993

Fig 4.5. Numbers of animals seen on standardized transect walks at different times of the year in forest habitat in the Kambui Hills: 1992-1993

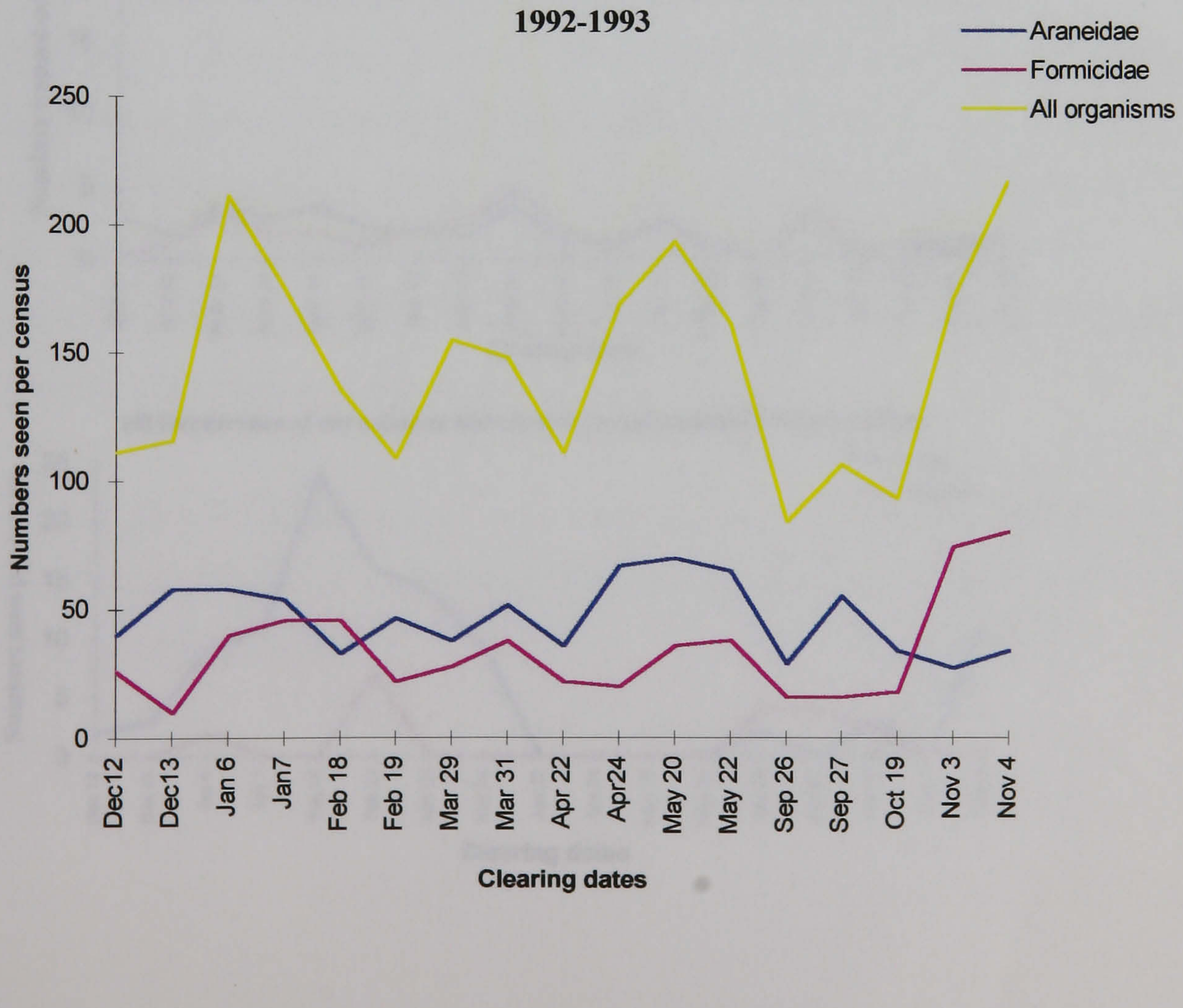
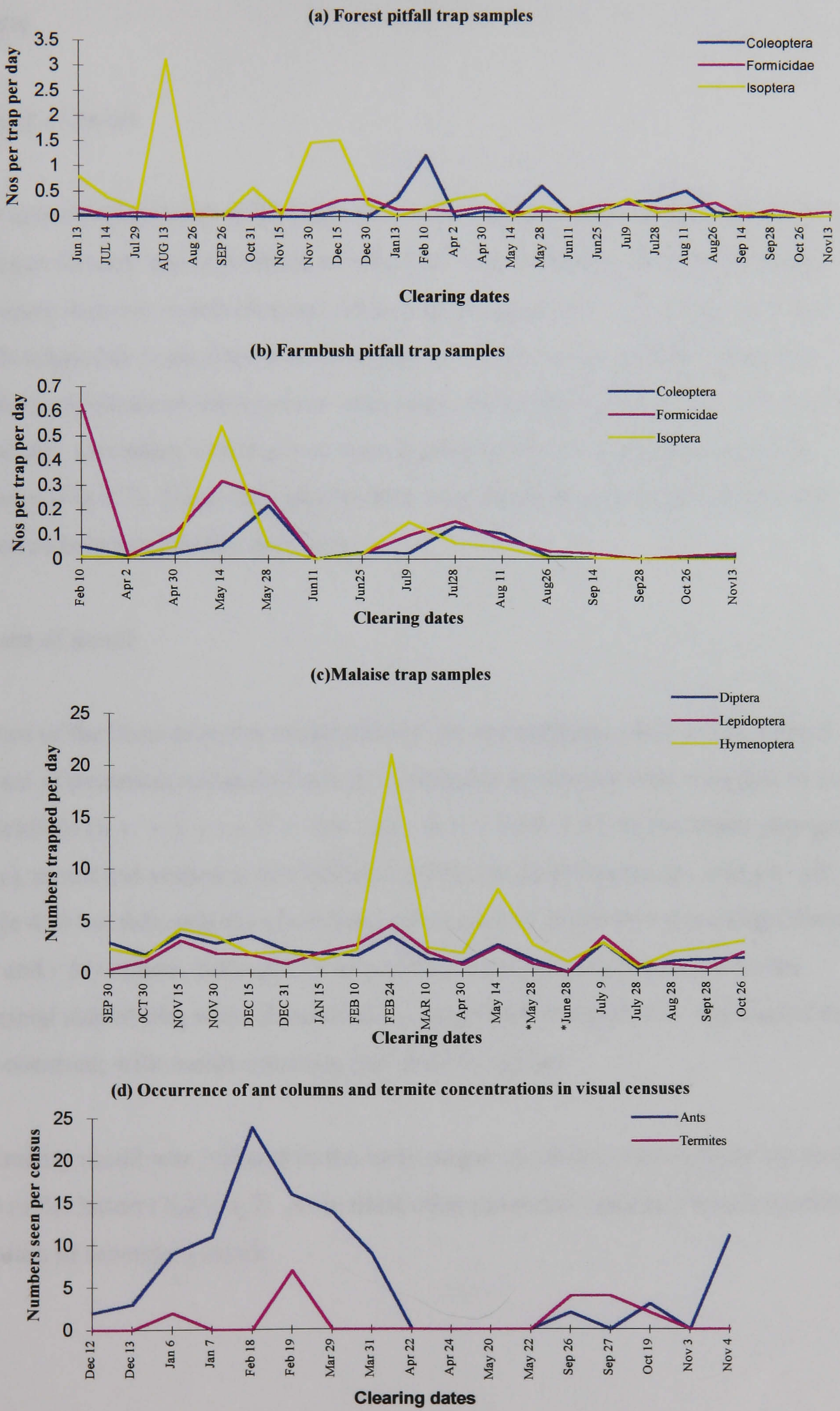


Fig 4.6. Seasonality of major animal groups monitored by different sampling methods in the Kambui Hills, 1992-1993.



4.4.2. The annual cycle

Moult

Timing of moult

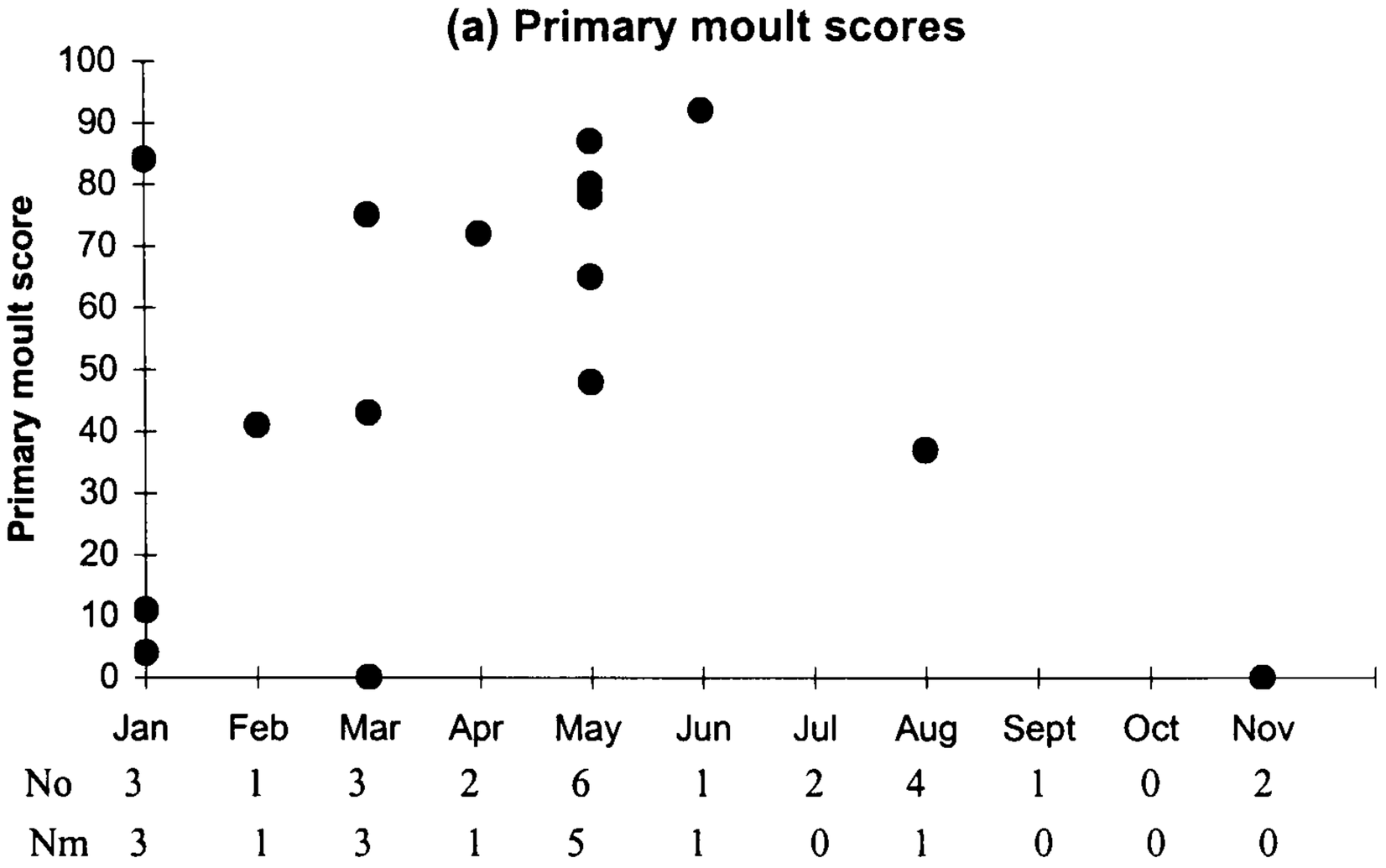
The state of wing moult of 25 adult *Picathartes gymnocephalus* were examined between January and November, of which 15 were moulting. Birds were found moulting in every month between January and August (n = 20), except July (n = 2). Birds trapped in September and November (n = 3) were not moulting (Fig 4.7). Primary moult scores were lowest in January and peaked between April and June. Similarly, secondary moult scores were highest in May, rising from minima in January (Fig 4.7). These data suggest that wing moult in *gymnocephalus* mainly occurred between January and June.

Pattern of moult

Eleven of the birds in active moult showed the normal descendent moult pattern typical of passerine remiges (Table 4.5.) Irregular sequences were recorded from four individuals (*w y; w y w / y; b r / b w and r bl / r*: Table 4.5). In two cases (*w y and w y w / y*), moult had started at two different points on the primaries (p1 and p4 - p6; Table 4.5) but followed the usual descendent pattern. In the two remaining cases (*b r / b w* and *r bl / r*) new, fully-grown or growing inner primaries occurred on the proximal side of old, worn distal feathers suggesting that partial or interrupted moult had occurred; with moult restarting just prior to capture.

Secondary moult was initiated in the early stages of primary moult (between scores 10 - 30 of the latter) (Table 4.5). As in most other passerines, primary moult spanned the duration of secondary moult.

Fig 4.7. The primary and secondary moult scores of *Picathartes gymnocephalus* at different times of the year. Figures below the x-axis in Figure 4.7a give the number of birds examined (No) and the number of birds moulting each month (Nm).



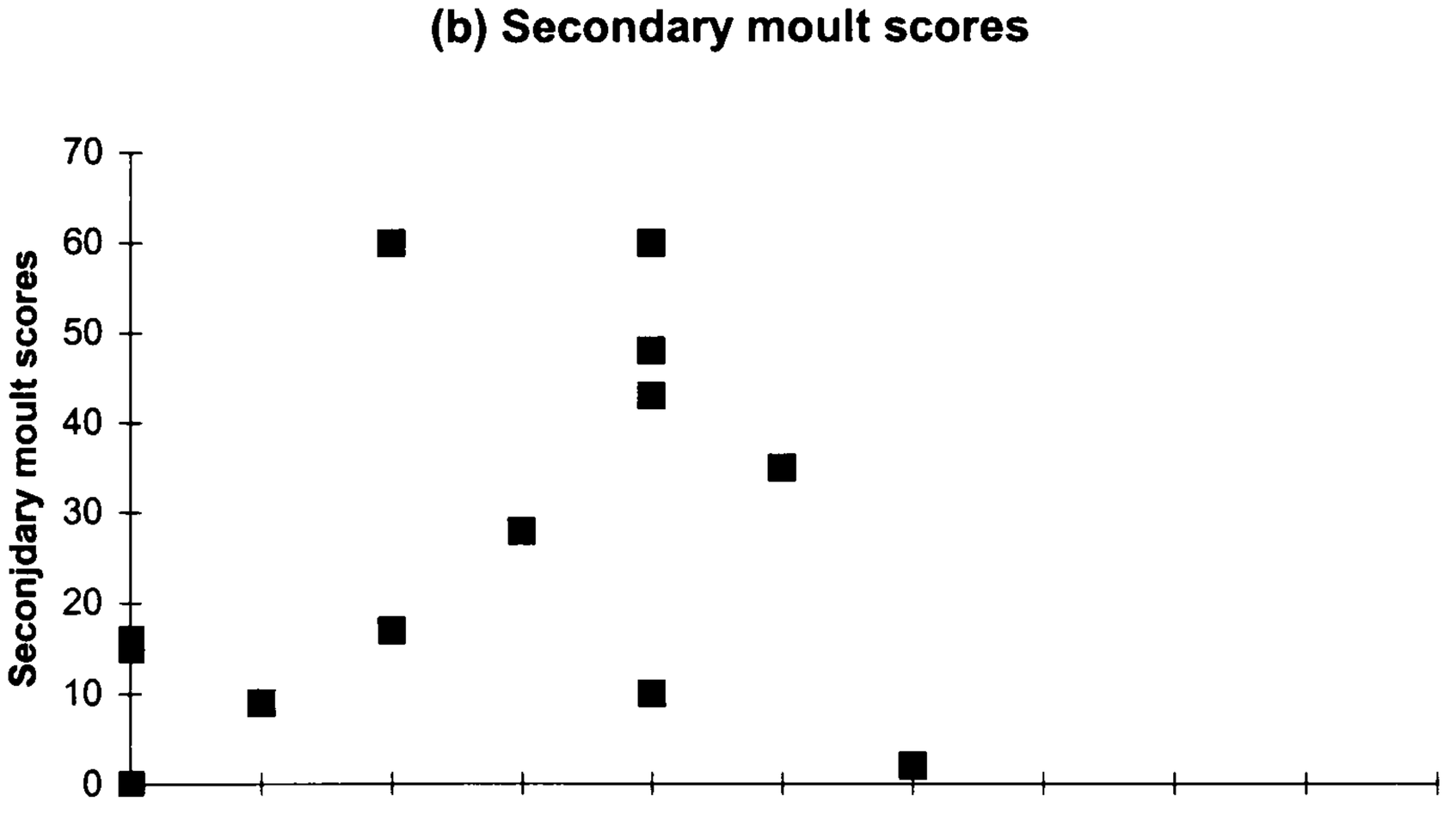


Table 4.5: Pattern of primary and secondary moult in *Picathartes gymnocephalus*

Colour ring combinations	Primary score	Secondary score
w y ;	2000023455	000002
	2000003555	230002
w r w ;	5555300000	504000
	5554100000	503000
w g w; y	5555555200	All new
	5555555300	
w o w; y	All old	All old
;bl y	5555554200	554000
	5555554200	554000
;w bl	5555555400	All new
	5555555400	
*w o w; y**	5555543000	555300
	5555544000	555555
g r ; w	5555555200	All new
	5555555555	
w g w; y	5555555500	553000
	5555555500	555555
w y w; y	2535555400	54000
	542003000	10000
g r w; y	All new	All new
dbl w; r g	4000000000	All old
	All old	
b dbl; r dbl	5555555530	330010
	5555555420	540000
b r; b w	0003100002	300315
	0000300002	300000
r w; r	5555555551	555000
	5555555551	555500
r bl; r	0520000000	002000
	0000555555	000000
w bl; y	All old	All old
o bl; g	All old	All old

* Indicates retrap

Key:
r - red; w - white; b - black; Y - yellow; g - green; o - orange; dbl - dark blue; bl - blue
Letters preceding semi-colon represent rings on the right leg;
letters after semi-colon represent rings on the left leg

The breeding season

Data on the timing of breeding were obtained from 74 nesting attempts at 17 nests over four years (1990 - 1994). Egg-laying started in different months at different sites and also varied between years (see Section 4.4.3), but in general, eggs were laid between June and December (immediately after moult) with peak numbers in October (45% of all eggs laid; Fig.4.8). Chicks were in the nest from August to January with highest numbers being found in November. From February to May, there were no eggs or nestlings at breeding sites (Fig. 4.8).

4.4.3 The annual cycle in relation to environmental factors.

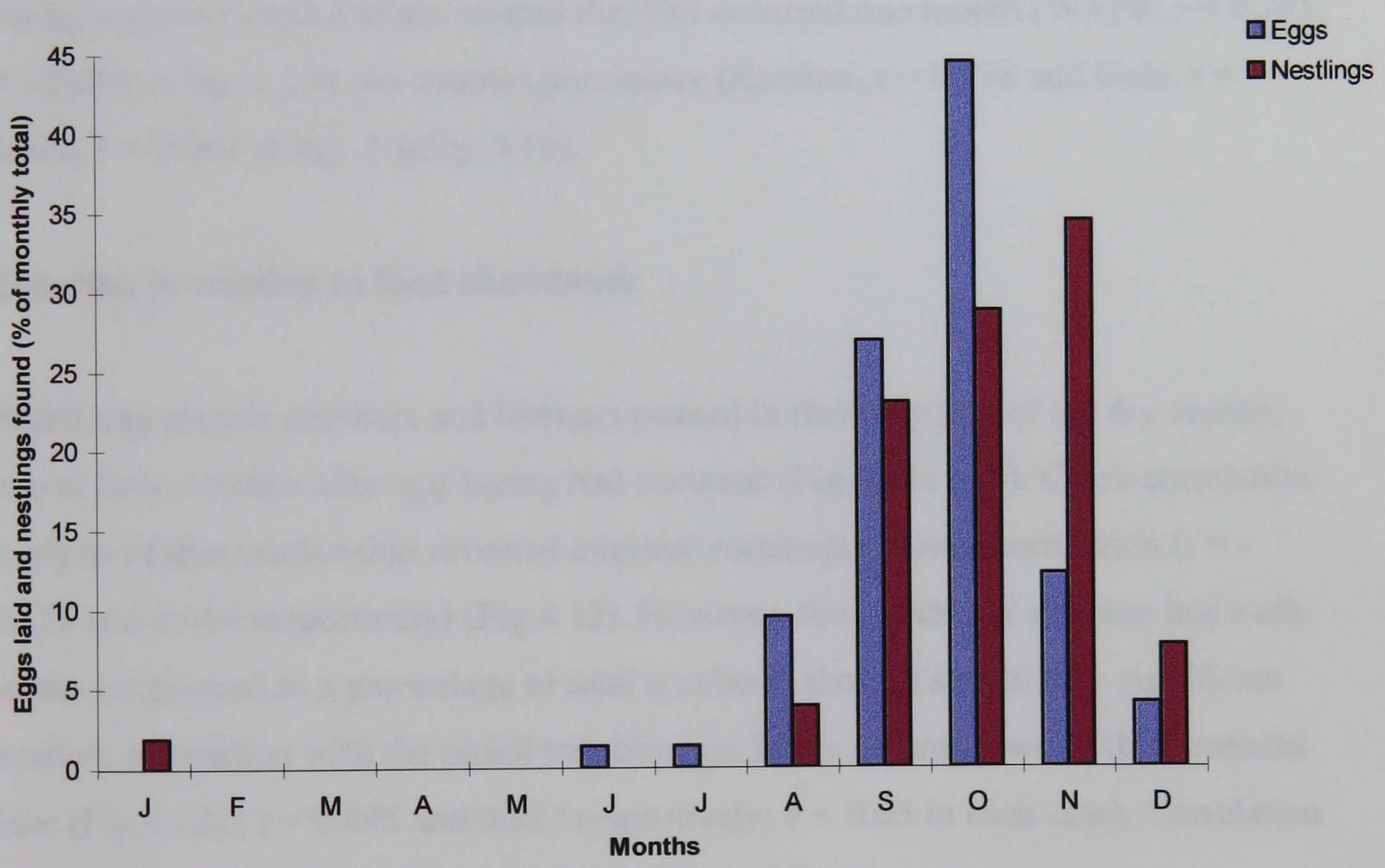
Cross-correlation analysis was used to investigate the relation between the timing of breeding at different study sites, and monthly rainfall and food levels. The procedure identifies any time delays to the correlation between two variables measured along the same time series (Wilkinson 1990). A correlation for a negative lag indicates the relation of the values in the first series to values in the second series that number of periods earlier. Similarly, correlations at positive lags relate values in the first series to subsequent values in the second series. The correlation at lag zero is the usual contemporaneous Pearson correlation.

Small samples sizes precluded similar site-based analysis for moult data. Moult data were therefore pooled and examined in relation to general patterns of breeding, rainfall and food abundance across all the study sites. Since moult is a fairly fixed temporal event in the annual cycle of birds (Dittami and Knauer 1986, Gwinner 1996), this approach should still provide useful information.

Breeding in relation to rainfall

Egg laying peaked in September or October, except in the WAPF in 1990 (August). The egg-laying peaks occurred one or two months after rainfall peaks at all sites (Fig. 4.9), but there were some site differences. Egg-laying started up to two months earlier

Fig 4.8. Numbers of *Picathartes gymnocephalus* eggs laid and nestlings found at different times of the year



in the WAPF (June) than in the Kambui Hills or Gola forest (earliest start of egg-laying, August). Also, egg-laying did not extend beyond November in the WAPF during the study period but continued into December in the Kambui Hills and Gola Forest (Fig. 4.9).

There was no significant correlation between breeding activity and that month's rainfall in the Gola forest ($r = 0.26$; $P > 0.20$) or the Kambui Hills ($r = -0.005$; $P > 0.5$; Fig. 4.10.). However, in the WAPF, this correlation was significant ($r = 0.454$; $P < 0.02$).

At all three study sites, correlation was strongest between the number of clutches laid during a given month and the rainfall that had occurred one month (WAPF: $r = 0.743$, $P < 0.001$ at lag -1) or two months previously (Kambui: $r = 0.738$ and Gola: $r = 0.621$, $P < 0.001$ at lag -2)(Fig. 4.10).

Breeding in relation to food abundance

Pitfall trap sample numbers and biomass peaked in the early part of the dry season, two to three months after egg-laying had occurred (Fig 4.11a & b). Cross-correlation analysis of this relationship revealed minimal contemporaneous correlation ($r = -0.128$ and 0.084 respectively) (Fig.4.12). However, the number of clutches laid each month (expressed as a percentage of total numbers) showed statistically significant positive correlation with the pitfall trap biomass levels recorded two to three months later (Fig.4.12) ($r = 0.495$ and 0.527 respectively; $P < 0.05$ in each case). Correlation with pitfall trap numbers was not statistically significant.

Fluctuations in malaise trap catches (numbers and biomass) did not show any discernible relationship with breeding seasonality (Fig 4.11 and 4.12).

It is possible that the egg-laying correlations with rainfall 2 to 3 months earlier may have been related to lag correlations betwwen food levels and rainfall (See previous Section: Breeding in relation to rainfall). However, there was no significant correlation between food abundance levels in the Kambui Hills (as measured by visual

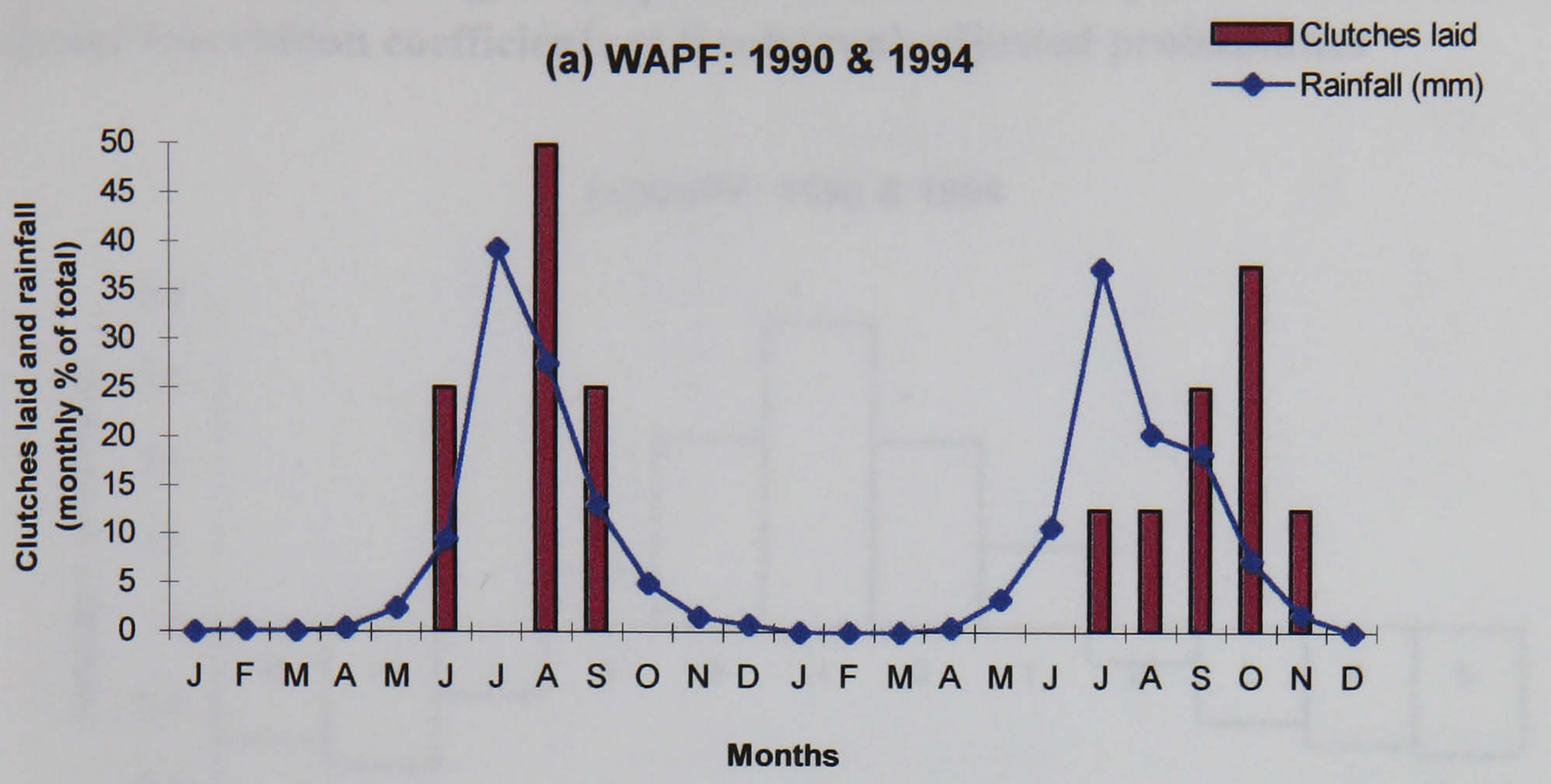
counts of prey and pitfall trap biomass) and rainfall 1 to 3 months earlier ($p>0.05$ in all cases).

Primary moult in relation to breeding and rainfall.

The proportion of birds found moulting each month at all study sites during the study period (1990 - 1994) is shown in relation to similar data for breeding seasonality and rainfall in Fig.4.13. Food abundance data were not available in similar form and are therefore not represented.

There was clear temporal separation of moult and breeding in the study population with most birds moulting between January and May (the dry season) after the period of egg-laying ended in December. Egg-laying avoids the peak of the wet season (July - August), occurring mainly in October and November as the rains tail off.

Fig 4.9. Relation between number of clutches laid (monthly % of total) by *Picathartes gymnocephalus* and monthly rainfall (mm)



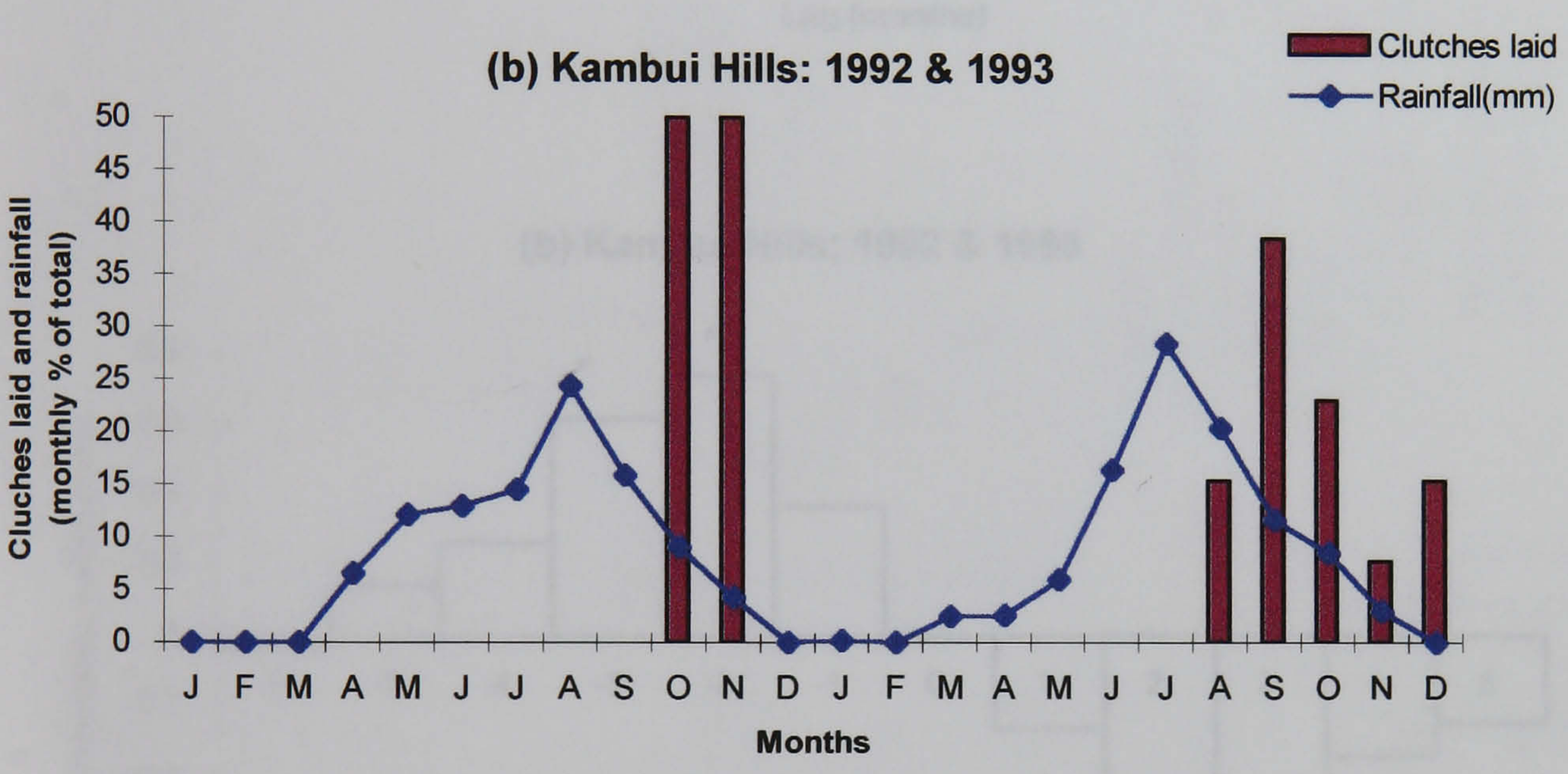
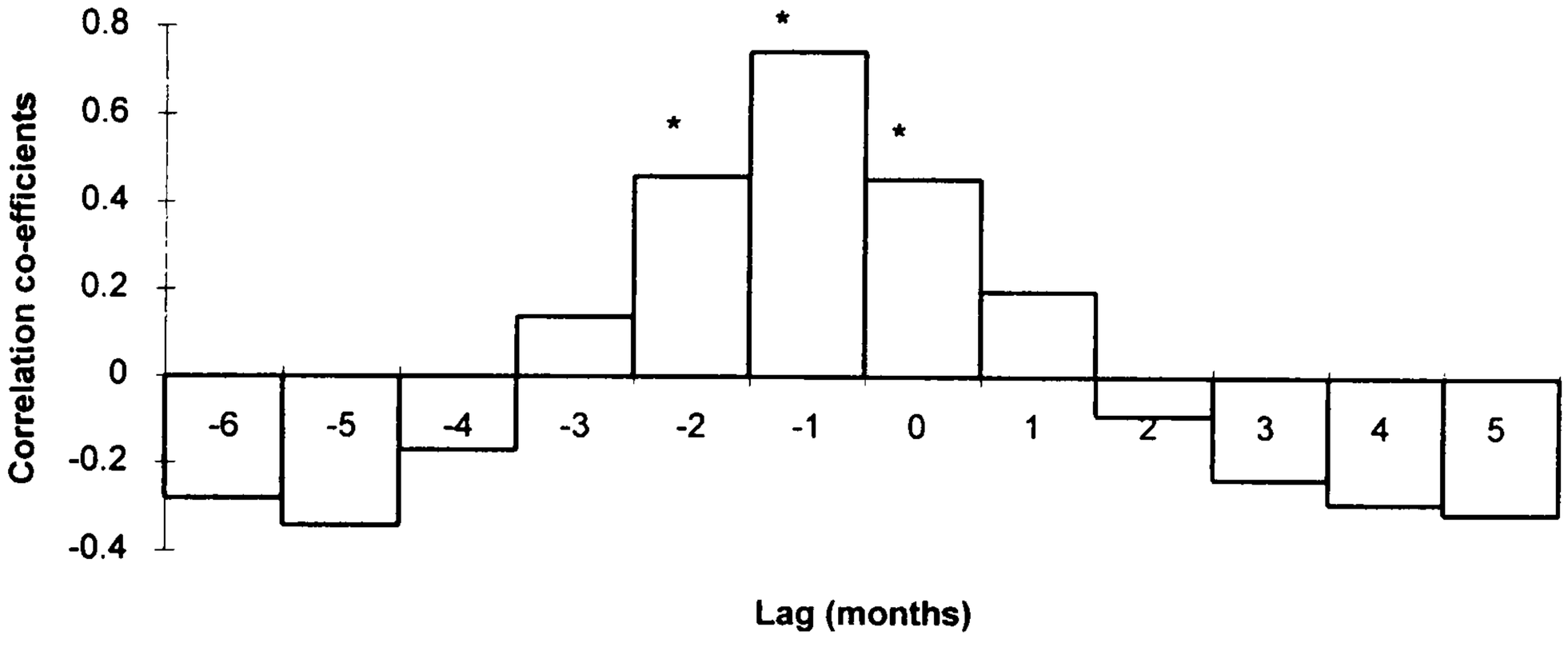
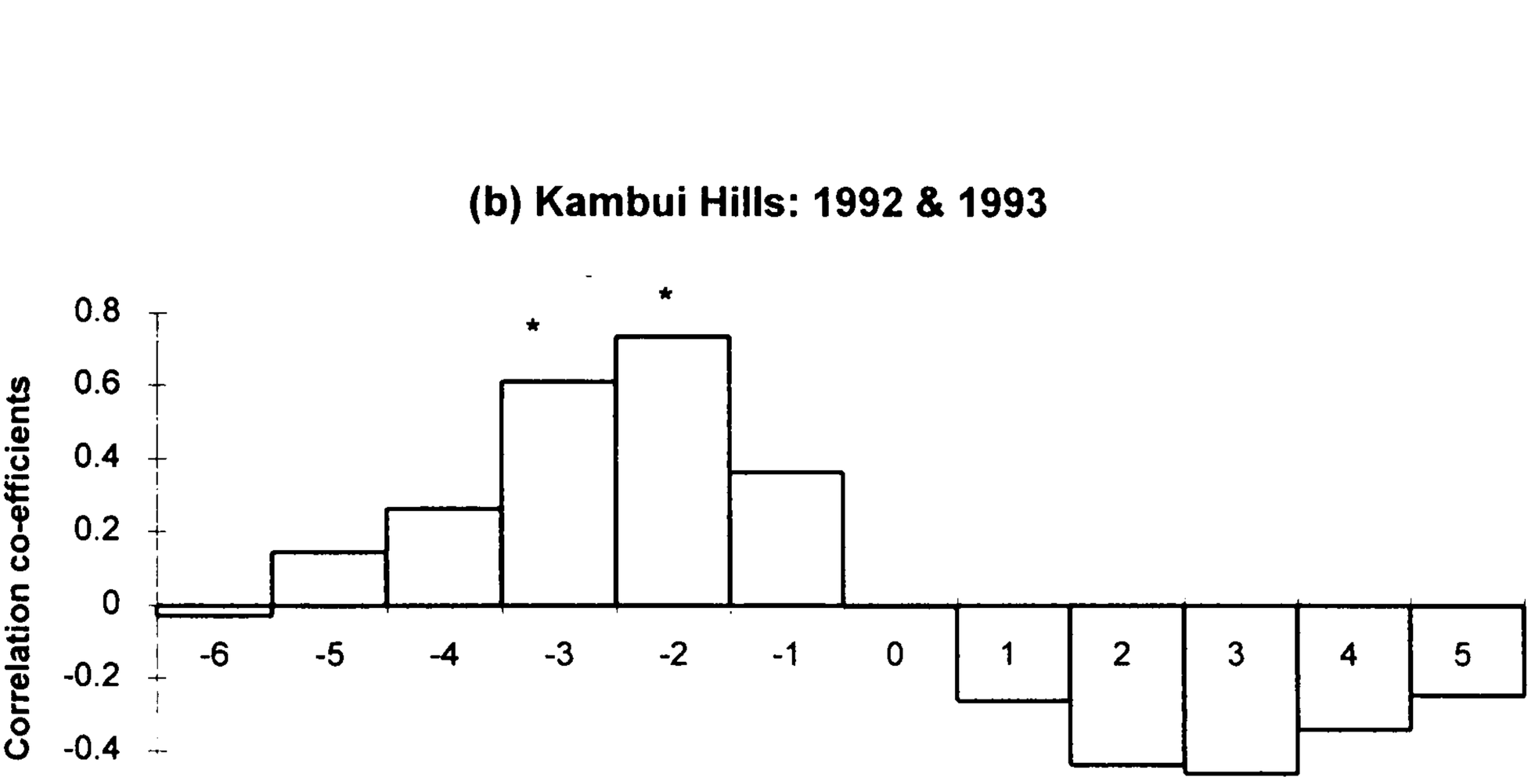


Fig 4.10. Cross-correlation analysis of rainfall and number of clutches laid each month (monthly % of total) by *P. gymnocephalus* at different study sites. Asterisks indicate significant correlation coefficients at Bonferroni-adjusted probabilities





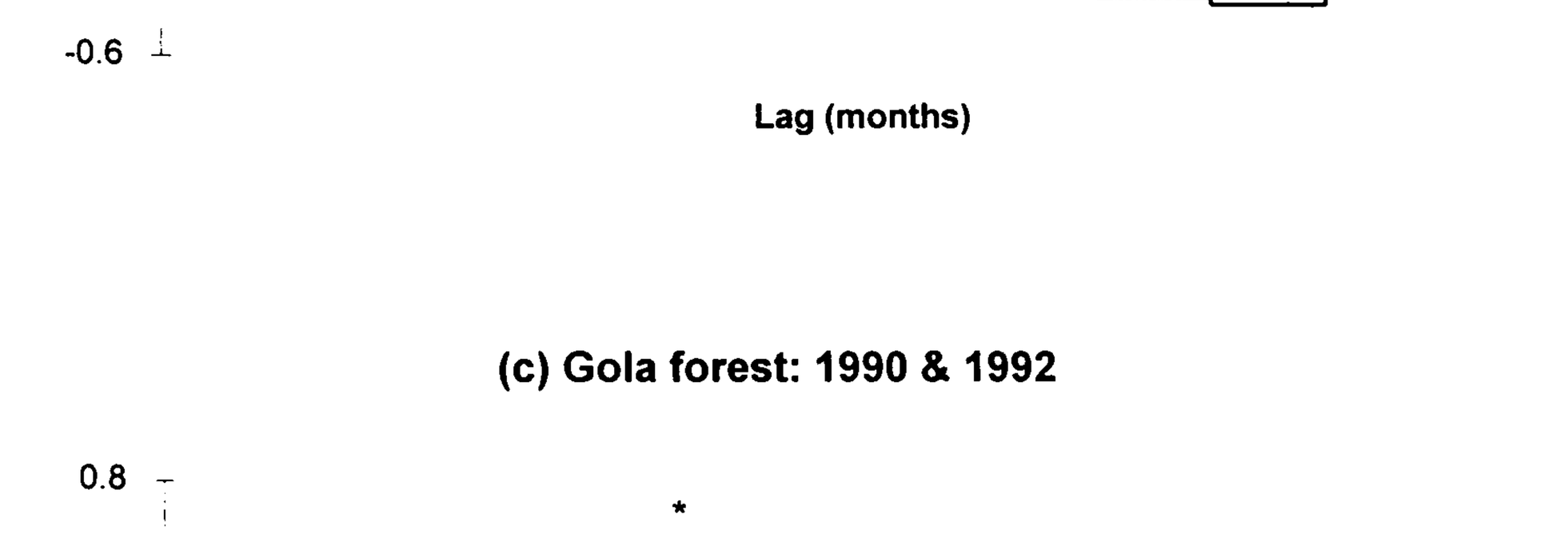


Fig 4.11 Relation between the number of clutches laid monthly (% of total) *by P. gymnocephalus* and seasonal fluctuations in food abundance levels in the Kambui Hills: 1992 - 1993

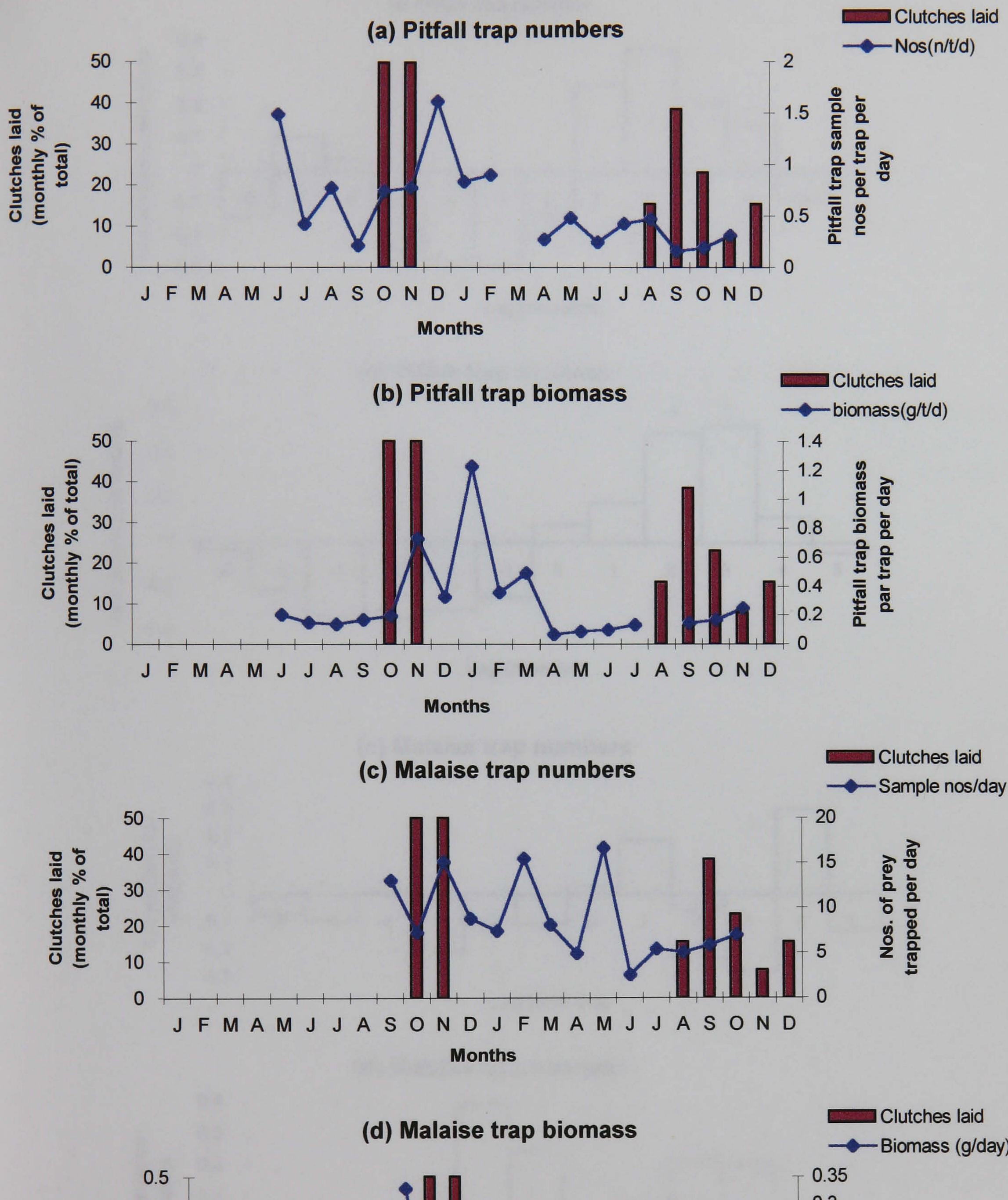
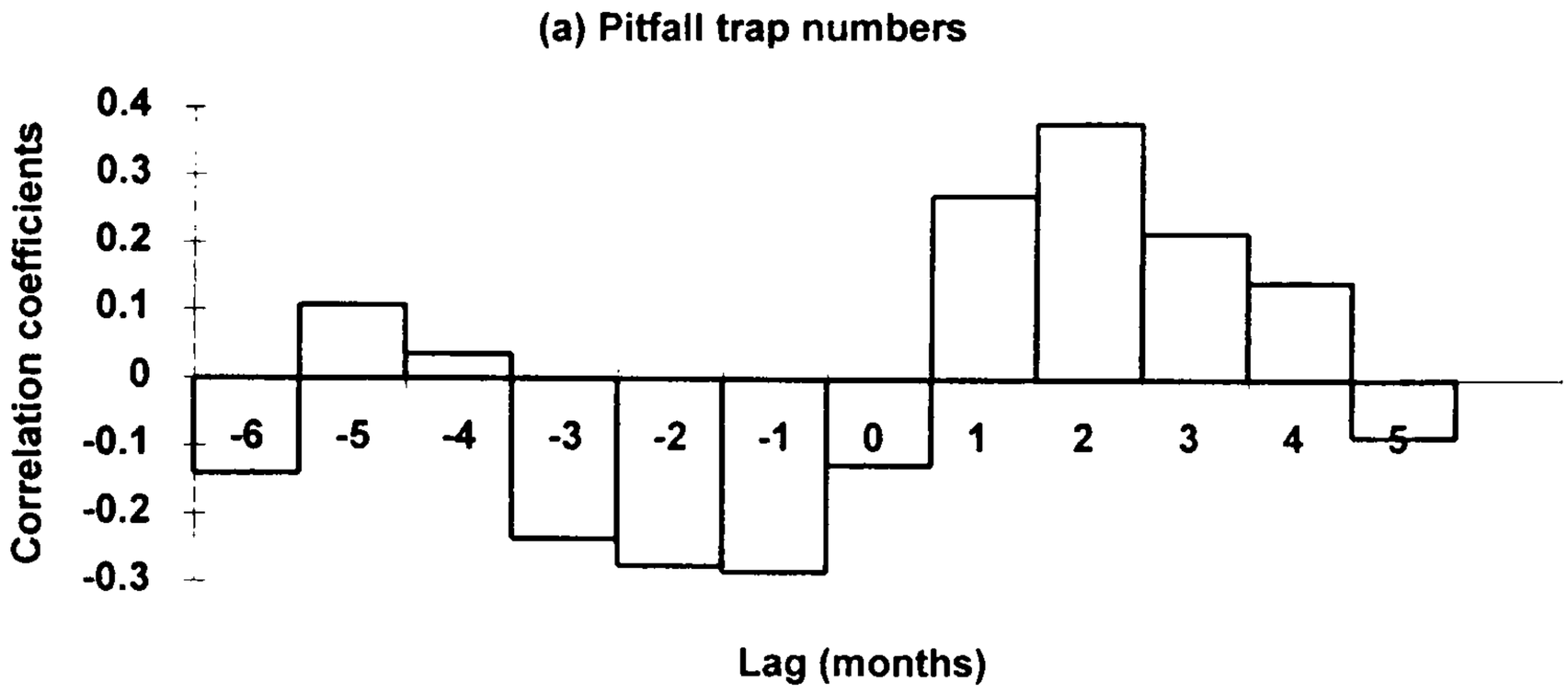
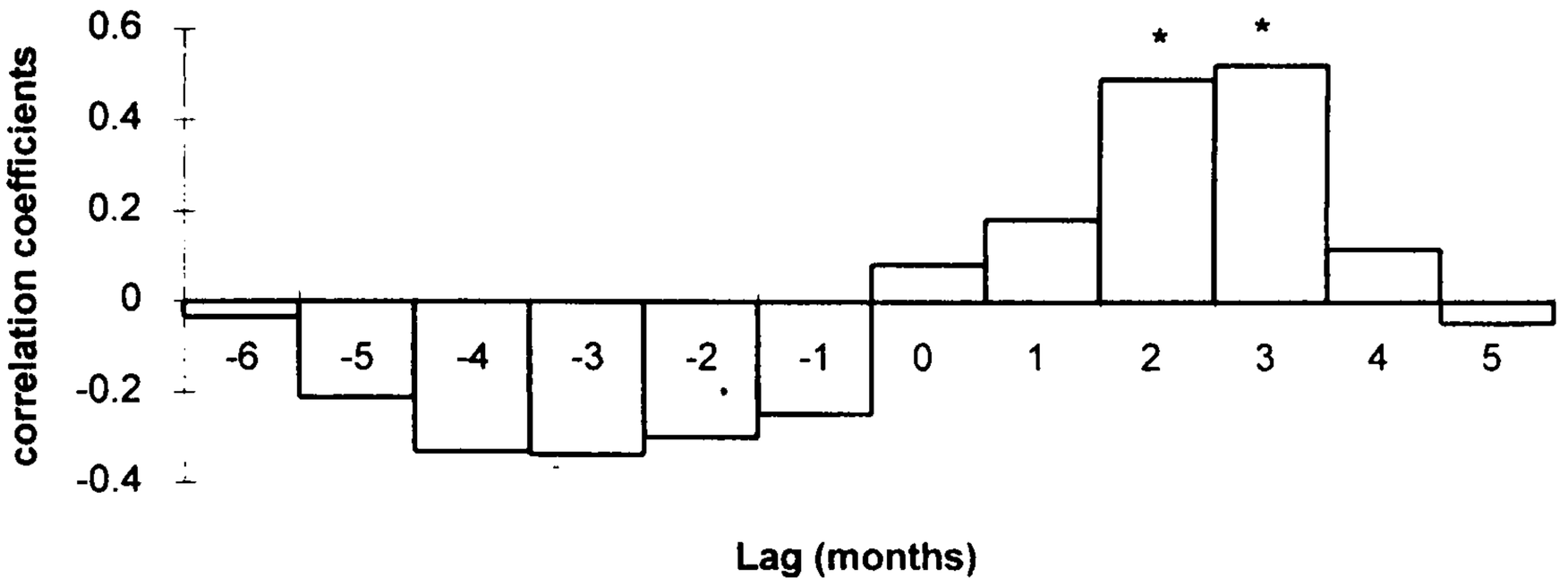
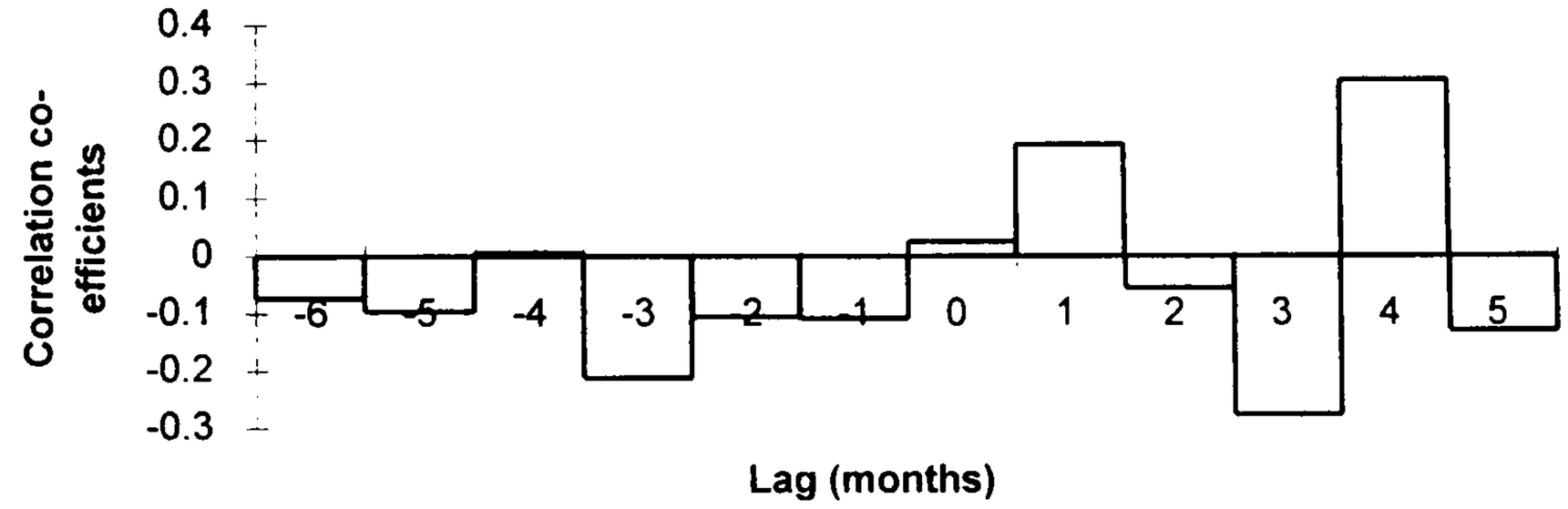


Fig 4.12. Cross-correlation analysis of food abundance levels and reproductive ouput of *P.gymnocephalus* (monthly % of total no. of clutches laid) in the Kambui Hills: 1992-1993







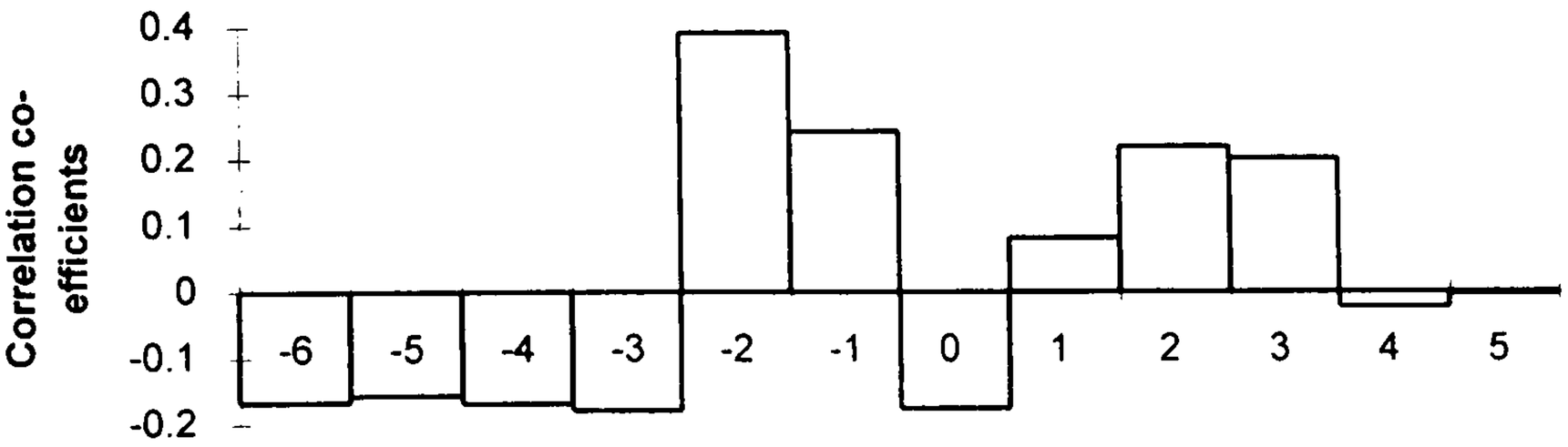
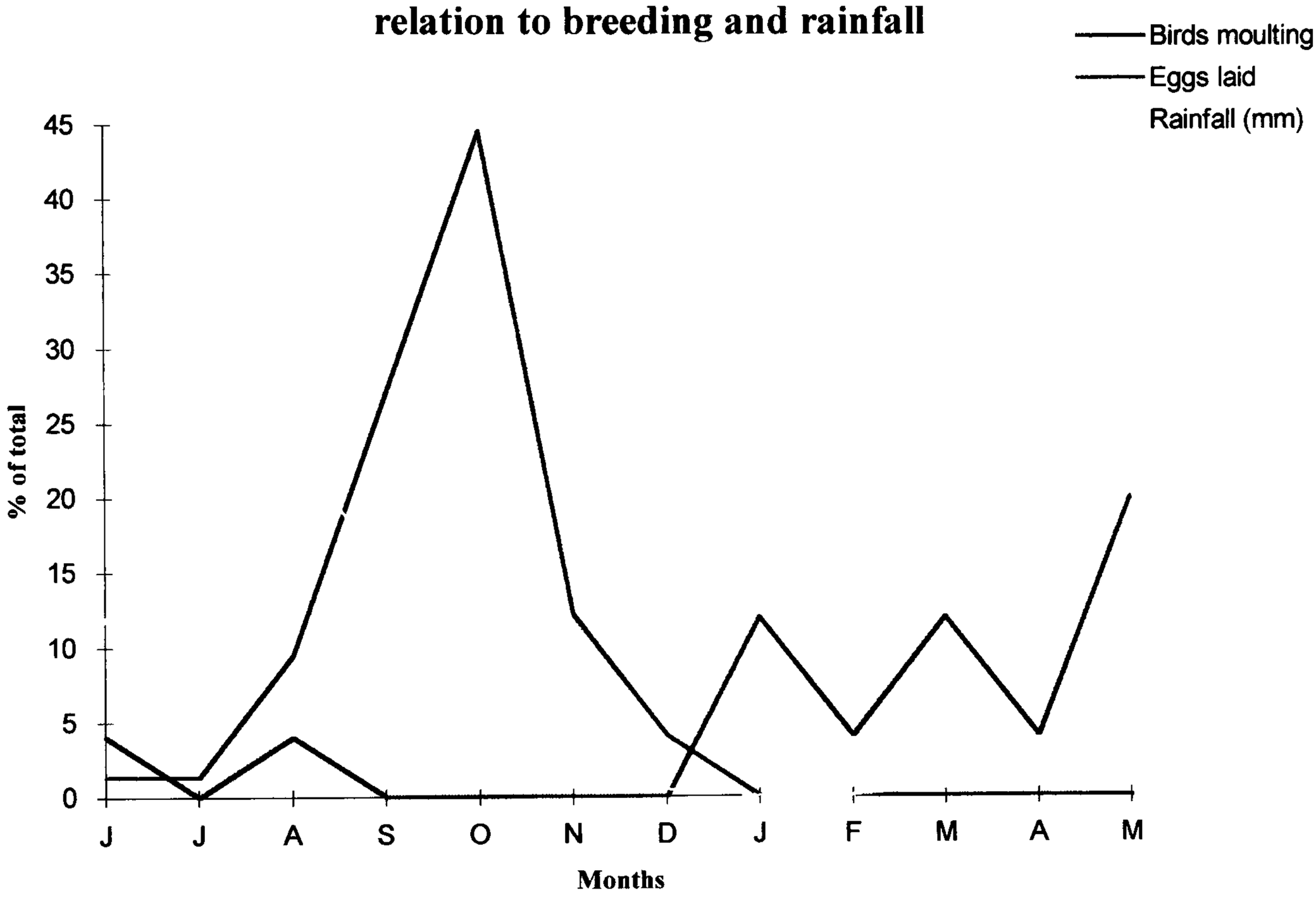


Fig 4.13. The primary moult of *Picathartes gymnocephalus* in relation to breeding and rainfall



4.5. DISCUSSION

4.5.1. Environmental Factors

Sampling Methods

Most standard methods for sampling invertebrate abundance are known to be biased to some extent (Cooper and Whitmore, 1990; Ausden, 1996). Capture or detection efficiency of each method differs among target species and the various methods differ in their efficiency in capturing a given species (Wolda, 1990). The efficiency of each method may also vary with habitat structure and ground cover (Greenslade, 1964). This has often led to difficulties in determining the biological relevance of catch results (Holmes, 1990; Hutto, 1990). However, when the objective of a study is to measure overall abundance of all arthropods in the same location over time, (such as in this study), then the techniques used here (among others) should suffice, because the inherent biases of a sampling method against certain prey taxa should be more or less constant (Cooper and Whitmore, 1990). This also applies to the potential confounding effect of habitat structure and ground cover (Ausden, 1996). On the other hand, relative abundances of species in a sample may have little relation to relative abundances in nature and therefore provide unreliable estimates of total abundance and how this changes with time Wolda (1990). When the objective is to measure prey availability for bird species, several other confounding variables may operate, including prey perception and acceptability to the birds and rate of turnover in the standing crop of prey (Hutto, 1990).

Given these caveats about faunal sampling methods, the results of this chapter (and those of chapter 5) are interpreted with extreme care. Changes in abundance of one set of taxa are not taken as "representative" of those in another. Emphasis is placed on general trends which occur in all three methods used. Such trends are more likely to reflect actual changes in abundance in nature. Also, because the sampling methods used, do monitor faunal abundance in the microhabitat (undergrowth) most frequently

used by *Picathartes gymnocephalus*, this makes it more likely that the data reflects changes in actual potential prey availability (Wolda, 1990).

Differences among sampling techniques

The three different sampling techniques produced different profiles of the forest undergrowth fauna. A high proportion of the malaise trap catch comprised winged hymenopterans, dipterans and lepidopterans all of which were either absent or occurred in relatively low proportions in pitfall traps (Tables 4.1 and 4.3). Surface active fauna (ants, beetles and termites) dominated the pitfall trap catch. Ants were also recorded in large numbers by visual censuses (Table 4.3) which also sampled the forest floor but spiders which were the most abundant organisms in the visual surveys occurred in relatively low proportions in pitfall traps. Both pitfall traps and visual surveys recorded vertebrates which were absent from malaise trap samples but only visual surveys recorded lizards and skinks. These differences were due to differences in the efficiency of each method in capturing/detecting different types of fauna but also reflected the fact that each method sampled a slightly different microhabitat. The malaise trap sampled low-flying or leaping insects during both night and day whilst the pitfall traps and visual censuses sampled forest floor fauna (only during the day in the case of visual censuses). Large, relatively mobile organisms with good visual acuity could either avoid the pitfall traps or escape from them (eg spiders, lizards, frogs). Such organisms were only detected in appreciable numbers by the visual censuses. On the other hand, relatively sedentary organisms which spent most of their time below or within litter such as earthworms were not easily detected on visual surveys (I could detect sudden or rapid movement more easily on census walks). Also, Lepidoptera were absent from the visual survey results because they moved away as the observer approached. Conclusions in this study about seasonal patterns and relative abundances of different taxa, are therefore based on more than one sampling method wherever possible.

Causes of the observed patterns

Some of the observed patterns in the variations in the abundance of the fauna were common to all three monitoring methods, to the two habitats sampled and also to the major groups in the samples. The most conspicuous of these were increased abundances at the onset of the wet season (May) and lower than average abundance levels in the middle and latter half of the wet season (Figs 4.2, 4.3, 4.5. and 4.6). Pitfall traps and visual surveys showed increased catch/detection levels at the start of the dry season but this was not the case for malaise trap catches.

Similar patterns have been observed in other studies (Owen, 1969; Dingle and Khamala, 1972; Boinski and Fowler, 1989; Frith and Frith, 1990) and it has been suggested that such patterns are primarily due to fluctuations in rainfall (Boinski and Fowler, 1989; Frith and Frith 1990). Heavy rainfall tends to decrease detectable litter and soil invertebrate densities by physically washing organisms away, forcing some to move deeper into the soil or into relatively sheltered microenvironments, and preventing foraging, mating and oviposition (Frith and Frith, 1990). These effects could have accounted for all or part of the reduction in invertebrate abundance observed toward the middle and latter half of the wet season in this study.

The amount of rainfall may affect invertebrate numbers indirectly, by influencing soil and litter moisture content which in turn affect plant growth and litter decomposition rates. The onset of the wet season stimulates new plant growth which increases the availability of food and water to soil fauna (Dowsett and Dowsett-Lemaire, 1984; Boinski and Fowler, 1989). This may have been partly responsible for increased abundance levels at the start of the wet season in this study. Some populations (eg termites, mosquitos, frogs) may also have life-histories which are affected by rainfall, with development being triggered by increased soil moisture and/or the presence of pools of water, leading to increased numbers at the start of the wet season.

The causes of the observed abundance peaks at some point in the early dry season (November to February) may have been due to increasing litter accumulation

(Hopkins, 1966; John, 1973; Songwe *et al,* 1988) at a time when the soil was still moist (Buskirk and Buskirk,1976). Also, in lowland tropical forest, a second flush of new vegetation is produced near the end of the wet season (Boinski and Fowler, 1989) This would have boosted food availability for many animals in the early part of the dry season. Abundance may have declined toward the latter part of the dry season because the soil got drier and the supply of fresh vegetation declined.

Comparison with other studies

Although comparable studies on under-storey fauna in African forests are apparently lacking, peaks in abundances at the onset of the wet season have been reported from other habitats. Owen (1969) reported a well-defined seasonal peak in the numbers of Sphingidae (Lepidoptera) captured by malaise and light traps at the beginning of the rains in May - June in open "garden-type " habitat in Sierra Leone. Dingle and Khamala (1972) recorded increases in numbers and biomass of insect sweep net samples at the start of the long rains on Kenyan grasslands whilst Critchley *et al* (1979) noted a build-up of the overall activity of crickets (Orthoptera) with the onset of the early rains in farmbush in Nigeria. Similarly, Dittami and Gwinner (1985) pointed out that the onset of heavy rains in Kenya was contemporal with a peak in flying insects and an increase in the abundance of pitfall-trapped insects.

Outside Africa, evidence for arthropod abundance peaks in the early rainy season in tropical forests has been well-documented (eg Fogden 1972, Buskirk and Buskirk 1976, Boinski and Fowler 1989, Karr 1990)

There is less corroboration for the reduction in the numbers and biomass of fauna during the rains observed here. In Africa, Dingle and Khamala (1972) noted a four-fold increase in the biomass of sweep-netted insect fauna during the rains over that recorded in the dry season. According to Critchley *et al* (1979) more crickets and millipedes (Diplopoda) were caught in pitfall traps during the rains than in the dry season whilst catches of ants and spiders did not show any marked seasonal trend.

In the neotropics, Boinski and Fowler (1989) found that arthropod abundance in lowland tropical forest in Costa Rica was lowest in the middle of the wet season but elsewhere, other workers have reported increased arthropod abundance during the wet season (Janzen and Schoener, 1968; Fogden, 1972; Buskirk and Buskirk, 1976). However, in a recent review, Tye (1996) concluded that arthropod increases during the wet season are not the major pattern in the tropics. Apparently, in lowlands lacking a severe dry season, many arthropod orders peak in drier periods, (possibly because the dry season is not severe enough to make moisture a limiting factor on plant and animal growth) (Tye 1996).

In this study, army ant columns and termite concentrations were most frequently recorded during the dry season (numbers seen peaked in February - Fig 4.6d). Studies from elsewhere do not as yet present a clear picture of seasonality in army ant activity. Dowsett and Dowsett-Lemaire (1984) state that army ants were much more active in the rains than in the dry season in Malawi. In Mexico, Coates-Estrada and Estrada (1989) noted that swarms of two species of army-ants were active all year round in tropical rain forest but they recorded the highest numbers of swarms per month in the driest months of the year. Tye (1996) recorded army ants most frequently from November to February (just after the driest period of the year). Army ants are predators of forest floor insects (Willis 1983) and it would be expected that swarming would be most frequent during periods of peak insect activity/abundance. Insect abundance as measured by pitfall traps was highest during this study from November to December, immediately prior to the peak in army ant activity (Fig 4.2)

Differences between habitats

Data for farmbush habitat in this study are derived entirely from pitfall trapping and any comparison with the forest needs to be treated with caution because of the effect of habitat structure on pitfall trap efficiency (Greenslade, 1964; Ausden, 1966). It is however worth noting that theoretically, the clearing of forest vegetation should result

in a decrease in the diversity and abundance of invertebrate fauna. Clearing involves simplification of the habitat with consequent reduction in diversity of food sources and nesting or oviposition sites (Critchley *et al,* 1979). The protection the forest canopy and dense vegetation affords against fluctuations in microclimate is lost, resulting in greater extremes of soil temperature and moisture, higher insolation and exposure to direct impact of heavy rains. This should affect smaller sedentary organisms more than larger more active ones. The results I obtained did not conform to the expected pattern. Mean numbers per sample trapped in farmbush were one and a half times greater than in forest and biomass was two times greater than in forest, although these differences were not significant (Table 4. 2). These results suggest that invertebrates were either more active in farmbush, were caught more easily by pitfall traps in this habitat or were actually higher in numbers and biomass in farmbush than forest. Owen (1969) also recorded higher arthropod catches in open habitat in Sierra Leone than in adjacent forest. These results merit further investigation. There are potential conservation implications. If food availability for *Picathartes* and presumably other forest ground-storey insectivores are not lowered by forest clearance, then the threat this activity poses is probably a consequence of direct disturbance (during clearance and the farming period) and/or increased predation risks as a result of the loss of cover.

4.6.2. Annual cycle

Comparison with other studies

Egg-laying by *P. gymnocephalus* mainly occurred in the latter part (September - October) of the wet season (May - October) and often continued into the first part (November - December) of the dry season (November - April)(Fig. 4.9). This supports previous suggestions, that in Sierra Leone, *gymnocephalus* breeds once a year in association with the wet season (Glanville 1954). It is not in agreement with previous reports that eggs were laid twice a year; once in the dry season (February to May) and once in the wet season (September - December) (J.S. Sawyerr *in litt* to L. Grimes, 1965). It also differs from the pattern of breeding by *gymnocephalus* in

Ghana where the birds breed biannually, apparently in response to the bimodal rainfall pattern (Grimes and Darku, 1968). It seems likely that the differences in the breeding patterns of *gymnocephalus* in Sierra Leone and Ghana can be circumstantially ascribed to the differences in the rainfall patterns in the two countries.

Within Sierra Leone, variations in timing of breeding by *P. gymnocephalus* corresponded with differences in rainfall between localities. In eastern Sierra Leone, the wet season is more prolonged than in the west, with rainfall in February and March (months conventionally regarded as the driest in the year; Fig 4.1) routinely exceeding 10mm a month. In this study, egg-laying in eastern Sierra Leone (Kambui Hills and Gola) extended into December but ended in November in the Western Area (Fig. 4.9). Also, casual nest inspection in the course of other work during this study (Chapter 6), resulted in the discovery of a *gymnocephalus* nest with two eggs, in May, in the Dodo Hills in eastern Sierra Leone. Previous reports of egg-laying by *gymnocephalus* in the dry season were also from eastern Sierra Leone (Grimes and Darku 1968, Allport 1989). As Tye (1987) has already pointed out, these records are probably a consequence of the prolonged wet season in this area.

Picathartes oreas is also generally known to breed in the wet season (Brosset 1965, Serle 1981, Ash 1991, Fotso 1992). However, Tye (1987) recorded *oreas* breeding on Mount Cameroon in the middle of the dry season (December -January) and drew attention to a similar record for *gymnocephalus* on Mount Nimba (Colston and Curry-Lindahl, 1986). She suggested that in montane areas the two species of *Picathartes* may breed in the dry season, because of the limiting effects of very high montane rainfall during the wet season. But Fotso (1993) noted that on the southwest slope of Mount Cameroon where Tye's study was done, there was usually some rainfall in December to February; months conventionally regarded as part of the dry season. This would mean that breeding of *oreas* on Mount Cameroon is also associated with rainfall and bears similarity to the situation in eastern Sierra Leone. The breeding biology of *Picathartes* (Chapter Three) suggests that breeding would be more difficult to carry out in the dry season. Nest building requires wet mud and one of the main

components of the diet of nestlings (lumbricid worms - Chapter Five) would be less accessible in dry soil.

In summary, it would appear that throughout its range, *Picathartes* breeds in the wet season (usually toward the end) and may vary timing of nesting in response to varying rainfall regimes. Moult occurred immediately after breeding, mainly in the dry season and was largely temporally separated from breeding (Fig 4.13). This pattern of events in the annual cycle is typical of many tropical passerine bird species (eg Ward, 1969; Diamond, 1974; Snow and Snow, 1974; Dittami and Knauer, 1986; Tye 1996).

Factors influencing the timing of breeding

Rainfall

The timing of events in avian annual cycles (breeding, moult and migration) is under the ultimate control of endogenous circannual mechanisms which are organized in a characteristic way for a particular species or population and to some extent genetically determined. These endogenous mechanisms however are synchronized with and modified by environmental factors in a complex way which results in an optimal adjustment to environmental conditions (Gwinner, 1996).

Various seasonally changing factors including photoperiod (eg Immelman, 1971; Murton and Westwood, 1977; Gwinner, 1996), food availability (eg Fogden, 1972; Jones, 1989a; Poulin *et al,* 1992), and rain (eg Dittami and Gwinner 1985) have been postulated as the proximate cues which impinge on and modify the circannual clocks controlling the timing of moult and breeding (gonadal stimulation/regression). These cues may differ between species and habitat. In the tropics, factors associated with the alternation between dry and wet seasons (food availability and rainfall) have been most frequently suggested as acting as environmental synchronizers for the annual cycle.

The results of this study indicate that for *P. gymnocephalus*, rainfall was probably

involved at an early stage in the chain of events which led to the initiation of breeding. Heavy rainfall (> 150 mm monthly) regularly started in May each year (Fig 4. 1) increasing to a peak in July or August. Egg laying was initiated from June onwards and egg laying peaks consistently occurred one to two months after the peak monthly rainfall (Fig 4.9). Correlation was strongest between the number of clutches laid during a given month and the rainfall that had occurred one or two months previously (Fig. 4.10). Shifts in rainfall patterns between years in the Kambui Hills (1992/3) was accompanied by a shift in the timing of egg-laying (Fig. 4.9).

Several workers (e.g. Ward, 1969; Fogden, 1972) have rejected rainfall as a proximate cue for eliciting the initiation of breeding, on the grounds of unreliability and that heavy rains outside the breeding season failed to elicit nesting activity. The problem of irregularity largely does not apply to the rainfall regime in Sierra Leone (Fig 4.1) and the records of *gymnocephalus* breeding outside the usual breeding season (Allport *et al*, 1989; Tye, 1996; this study) may indicate responses to unseasonal rains.

Food Abundance

In seasonal environments, breeding by birds (defined as clutch initiation) is timed to coincide with peaks in food availability (Lack, 1968; Immelman, 1971; Worthington, 1982; Dittami and Knauer, 1986; Young, 1994). This maximises the chances of parents fulfilling the high energetic demands of reproduction. The most energetically demanding stage of reproduction may occur during egg production, nestling rearing, or in finding food to feed dispersing nestlings (Lack, 1954; Young 1994; Perrins 1996).

Of the prey sampling methods used here, pitfall trap catches and visual censuses were more similar to the diet of *gymnocephalus* than malaise trap catches (Chapter 5). Analysis of the relation between potential food abundance and breeding seasonality showed a statistically significant positive correlation between the number of clutches laid each month (expressed as a percentage of total numbers) and the pitfall trap biomass levels recorded two to three months later (Figs 4.11 & 4.12). Also, although

no statistical analysis was carried out, it was clear that the occurrence of ant columns and termite concentrations in visual surveys peaked one to two months (Jan - Feb) after the end of egg-laying (Fig 4.6d). Ants and termites were numerically important constituents of *gymnocephalus* nestling diet and *P. gymnocephalus* regularly forages at army ant columns for food (Willis 1983, pers obs). These results therefore suggest an increase in food abundance levels one to three months after egg laying by *gymnocephalus* - a period when adults were probably finding food for dispersing offspring. If co-occurrence of food peaks and the most energetically demanding stage of reproduction is an optimal strategy for *gymnocephalus*, these results may well mean that finding food for dispersing offspring is a limiting factor in energetic demands during the species' breeding cycle.

CHAPTER FIVE

THE DIET OF BREEDING *PICATHARTES GYMNOCEPHALUS*

5.1 AIMS

The main aim of the research described in this chapter was to identify the key food resources on which breeding *Picathartes gymnocephalus* depend. This should allow greater insight into how changes in the environment could potentially affect *gymnocephalus* populations - essential information for conservation and management.

The specific research questions were:

1. What do breeding adult *gymnocephalus* and their nestlings feed on ?

2. Do diets of adults and nestlings differ in prey type and prey size?

3. Are nestling diets related to their age?

5. How does *gymnocephalus* diet relate to relative food abundance in the environment?

5.2. PREVIOUS WORK

Sharpe and Bates (1908), Lowe (1938) and Walker (1939) each described the stomach contents of single specimens of *Picathartes* (*gymnocephalus* in the case of Walker and *oreas* for the other authors) with Lowe providing most detail (prey taxa identified below class level). Tye (1987) assessed the relative numerical contribution of different prey taxa to the diet of *oreas* nestlings (n = 2) and estimated relative prey size in relation to adult bill length. Apart from these early investigations, knowledge of *Picathartes* feeding ecology is limited to casual and incidental field observations (McArdle,1958; J.S. Sawyerr *in litt* to Grimes, 1965; Grimes 1963; Willis, 1983; Brosset and Erard, 1986; Fotso, 1993) or information obtained from captive birds (Glanville, 1954; Faust, 1970; Dekker, 1973).

There has not been any previous quantitative analysis of the diet of *Picathartes gymnocephalus*. Nothing is known of how any of the *Picathartes* species use food resources in relation to prey abundance in the environment; of dietary change with nestling age, or of differences in the composition of diets of birds resident in different areas.

5.3. METHODS

5.3.1. Diet analysis

The composition of the diet of adult and nestling birds was investigated by two methods: a) direct observation at nesting sites b) the analysis of faecal samples

Direct observation

Prey fed to nestlings at the Kambui Hills study site were identified during observations of breeding behaviour (220 hours; Chapter Three). Identification was usually made to the ordinal level. Prey sizes were initially estimated by expressing the longest dimension as a proportion of mean adult bill length (33.1mm ±0.3mm, n = 21; Chapter Three). Relative lengths were converted to absolute sizes by simple proportion and for some prey types (mainly non-insects), these dimensions were later used to estimate biomass using regression equations derived from length and weight measurements of specimens collected close to the study site (see Section 5.3.3).

Prey recognition could have been improved by placing ligatures around nestlings' necks to prevent their swallowing. However, this method may cause older nestlings to leave the nest prematurely and is known to affect nestling feeding behaviour and survival (see review by Rosenberg and Cooper, 1990). I therefore decided not to use this method in order to minimize the intrusion occassioned by handling nestlings for growth rate data (Chapter 3).

Faecal collection and analysis

Nestling faecal pellets were collected from below nests at nesting sites in the WAPF and Kambui Hills. Adult samples were also collected at nesting sites but only if (a) an adult had actually been seen defaecating (b) the faeces were found away from the usual area of nestling faeces deposition or (c) the faeces had been deposited at a time when there were no nestlings at the site concerned.

Individual samples were preserved separately in 70% alcohol in labelled specimen tubes and stored for later examination.

Each sample was later decanted into about 2 ml of water in an 18mm diameter petri dish, then broken apart very gently with dissecting needles. Five to ten sub-samples were prepared by decanting one-fifth to one-tenth of the original volume into another 18mm petri-dish which had a 2 x 2 cm grid attached to the base. This allowed systematic scanning. A further small quantity of water was added to each sub-sample so that it became less cloudy and clear enough for effective scanning.

Sub-samples were examined at magnifications of x10 to x30, using a binocular dissecting microscope. Identifiable plant or animal fragments such as heads, wings, legs, chelicerae, body segments, antennae and mandibles were removed for further examination. A special check (at x30 - x40) was then made for earthworm chaetae, wing scales from lepidopterans, vertebrate scales and any other items which could have been easily overlooked.

Identifiable fragments were mounted separately on glass slides and examined further at magnifications ranging from x40 to x400 with a microscope fitted with a micrometer eyepiece. Each fragment was measured, sketched and any conspicuous features noted. The diagnostic fragments and features used to identify and quantify different prey types are given in Appendix 5.1.

Identifiable fragments from the same sample were stored in a single labelled specimen tube. The remaining unidentified material from each sample was filtered through smooth filter paper (9cm), then air-dried and stored in 70% alcohol.

Each faecal sample took 2-5 days to process and was examined 2-3 times. Complete examination of all samples was carried out over three years. Two research assistants were trained to isolate potentially diagnostic fragments and helped with the process during the last year.

Most prey were identified to order or sub-order, and a smaller proportion to family, using standard texts and keys (eg Borror and Delong, 1954; Webb, 1961; Borror *et al*, 1981), relevant papers (eg Ralph *et al*, 1985; Moreby, 1988) and a reference collection of potential prey collected in the study areas.

Discrete, distinctive prey remains were counted, matched and divided by the associated number per prey item to determine a minimum number of prey items (eg Tatner, 1983; Chesser, 1995). This was not possible for earthworms and millipedes because their most easily identifiable discrete structures (chaetae, legs) were numerous and the relationship between the numbers of these prey eaten and the number of discrete structures which would be expected to be found in the faeces was not known. In such cases, the best way to assess the relation between the numbers of discrete structures in the faeces and the number of prey eaten is to examine the faeces of a captive bird fed on a measured diet (eg Galbraith, 1989; Green and Tyler 1989). A correction factor is then calculated and used to convert the numbers of fragments found in the faeces to the numbers of whole animals eaten. This approach can be used for all frequently encountered prey taxa in faecal sample analysis. Given the nature of the study species, this approach was not possible here. I have therefore used the arbitrary assumption that 10 earthworm chaetae in a faecal sample represented one earthworm eaten (after Tatner 1983, Yalden 1986) and that five millipede legs represented one millipede eaten.

5.3.2. Measurement of potential prey abundance

Preliminary observations indicated that undergrowth fauna formed the bulk of *gymnocephalus* diet (Section 3.4.2.). The abundance of these organisms was monitored in the Kambui Hills by pitfall trapping, visual surveys and a malaise trap (see Chapter 4;. Section 4.3.2). The methods used in setting up and operating these traps and surveys have been described in Chapter Four.

5.3.3. Data analysis

Size estimation

Prey sizes were estimated using regression equations computed from measurements of organisms collected in the study areas or based on previously established length - weight relationships in the literature.

For insects and arachnids identified to ordinal level, taxon specific length-weight relationships given by Rogers *et al* (1977) and Calver and Wooller (1982) were used to obtain biomass estimates. For unidentified insects, the general relationship between insect body length and biomass given by Rogers *et al* (1976) was used ie W = $0.0305L^{2.62}$ (W = length in mg and L is length in mm).

Body lengths and dry weights were determined for earthworms, frogs, millipedes, and lizards collected in the vicinity of the Kambui Hills study site and the relationships between the measurements determined by regressions and correlations for each taxon (Section 5.4.2).

Prey size was estimated only for prey items seen delivered whole to nestlings. Adults often shredded large prey before feeding the nestlings. It was therefore felt that estimating prey size from remains in nestling droppings would not be very useful.

Comparison of diet composition and the catch composition of trap samples

In order to determine which of the three trapping methods used to assess potential prey abundance in the environment (pitfall traps, visual surveys and a malaise trap) produced a catch which most closely resembled *gymnocephalus* nestling diet, I used the Percentage Similarity or Renkonen Index, *PS* (Krebs 1989) to compare diet and trap catch compositions:

where $PS = (\Sigma \text{ minimum } (p1_i, p2_i)$, in which

PS = percentage similarity between samples 1 and 2

$p1_i$ = percentage of species i in community sample 1

$p2_i$ = percentage of species i in community sample 2.

This index ranges from 0 (no similarity) to 100 (complete similarity).

There are more than two dozen similarity measures (Magurran, 1988) but the Percentage Similarity Index was used here because it is simple to calculate, relatively unaffected by sample size and by species diversity and therefore considered one of the best quantitative similarity coefficients available (Krebs, 1989).

Prey selection

The degree of selection of food items by *gymnocephalus* in relation to environmental abundance was assessed by the Strauss Index (Strauss, 1979). This is a very simple index calculated as *ri* - *pi*, where *ri* is the relative abundance of food items in the birds diet and *pi* is the relative abundance in the environment. It ranges from -100% to +100% with positive values indicating preference and negative ones indicating avoidance or inaccessibility (Moreira, 1995).

The relative preferences of *gymnocephalus* for different prey taxa within the determined diet was investigated by determining a rank preference index for each prey taxon (Krebs, 1989). This was done by:

a) determining the rank of usage (r_i) of prey taxa from 1 (most used) to *m* (least used),

where m is the number of prey items in the diet.

b) determining the rank of relative abundance (s_i) of the m prey taxa in the environment.

c) calculating the rank difference for each of the m prey taxa as

$t_i = r_i - s_i$, where t_i = rank difference (measure of relative preference)

r_i = rank of usage of prey type i (i = 1,2,3,....m)

s_i = rank of relative abundance of the prey type i

d) ranking these rank differences to give an order of relative preference for all prey types in the diet. The smallest average rank difference indicated the most preferred resource.

5.4. RESULTS

5.4.1. Diet composition

Nestling diet from faecal analysis

A total of 2832 prey individuals were isolated from 151 faecal samples collected from the Kambui Hills (106 samples) and the WAPF (45 samples). These data are presented in terms of relative numerical abundance in three ways: as a percentage occurrence in all the 151 samples; as a percentage occurrence of all the prey occcurrences (959) and as a percentage of all the individual prey items identified (2832: Table 5.1). Each of these methods has drawbacks but all three provide a similar "picture" of nestling diet.

Six prey types - Coleoptera (beetles), Lumbricidae (earthworms), Isoptera (termites), Formicidae (ants), Araneae (spiders) and Orthoptera (crickets, mantids and grasshoppers) were the most important constituents of the diet in numerical terms. Together, they formed 64% of all prey occurrences. Each of these main prey groups occurred in between 35% and 96% of all samples and constituted from 2% to 36% of all prey individuals identified (Table 5.1). Beetles were the most commonly occurring prey in *Picathartes* nestling diet; they were present in 96% of samples, formed 15%

of the total prey occurrences and constituted 8.6% of the total number of prey identified (Table 5.1). Ten families of beetles (Carabidae, Scarabidae, Cinclinidae, Chrysomelidae, Elateridae, Nictidulidae, Byrrhidae, Sylphidae, Staphylinidae and Harpalinidae) were identified as part of *gymnocephalus* nestling diet with Carabidae and Scarabidae being the most common. Termites comprised mainly Rhinotermitidae. Identified families of ants were Dorylinae, Myrmicinae, Formicinae and Ponerinae. The army ants (Dorylinae) at whose columns adult *Picathartes* are known to forage (Willis, 1983), comprised 6% of 111 ant occurrences in nestling diet. Gryllidae, Tettigonidae and Mantidae were the orthopterans identified as being fed to nestlings.

Numerically, the second most important group of prey types in the diet comprised Anura (frogs), Diplopoda (millipedes) and Dermaptera (earwigs). These taxa together comprised 12% of all prey occurrences (range = 2-5%); 1-2% of the total number of individual prey identified and occurred in 17-31% of all samples (Table 5.1). Each of the remaining 23 prey taxa identified to the level of order or better, comprised less than 1% of the total number of individual prey identified; occurred as less than 3% of prey occurrences and were found in less than 12% of the total number of samples.

In general terms, *Picathartes* nestling diet was dominated by invertebrates, particularly insects, which formed 52.6% of all individual prey items identified. Earthworms were the main non-insect invertebrate prey and constituted 36% of identified prey items. Vertebrates (frogs and lizards) comprised only 2.2% of identified prey items and 6% of the total prey occurrences. Plant material was present in 3% of samples and consisted of moss and small bits of plant stem. These were probably taken incidentally when birds were foraging for animal prey or may have been accidentally included when samples were being collected.

Table 5.3. Diet of *Picathartes gymnocephalus* nestlings in Sierra Leone presented as percentage of total no. of samples, percentage of total number of prey occurrencies and percentage of the total number of individual prey identified.

Taxa	Prey occurrencies:									Prey individuals:					
	No. of prey occurrencies			% of samples			% of prey occurrencies			No. of prey individuals			% of total		
	Kambui	WAPF	Both sites	Kambui (n=106)	WAPF (n=45)	Both sites	Kambui (n=689)	WAPF (n=270)	Both sites	Kambui	WAPF	Both sites	Kambui (n=2265)	WAPF (n=567)	Both sites
Isoptera	84	29	113	79.25	64.44	74.8	12.19	10.74	11.78	309	90	399	13.64	15.87	14.1
Lumbricidae	84	40	124	79.25	88.89	82.1	12.19	14.81	12.93	878	142	1020	38.76	25.04	36
Formicidae	77	34	111	72.64	75.56	73.5	11.18	12.59	11.57	173	67	240	7.64	11.82	8.5
Araneae	57	14	71	53.77	31.11	47	8.27	5.19	7.4	89	16	105	3.93	2.82	3.7
Undet.Coleoptera	45	3	48	42.45	6.67	31.8	6.53	1.11	5	70	7	77	3.09	1.23	2.7
Anura	44	3	47	41.51	6.67	31.1	6.39	1.11	4.9	48	4	52	2.12	0.71	1.8
Orthoptera	29	24	53	27.36	53.33	35.1	4.21	8.89	5.5	45	43	88	1.99	7.58	3.1
Dermaptera	24	2	26	22.64	4.44	17.2	3.48	0.74	2.7	38	2	40	1.68	0.35	1.4
Diplopoda	23	19	42	21.70	42.22	27.8	3.34	7.04	4.4	29	24	53	1.28	4.23	1.9
Scarabidae	15	16	31	14.15	35.56	20.5	2.18	5.93	3.2	22	36	58	0.97	6.35	2.05
Carabidae adults	13	28	41	12.26	62.22	27.2	1.89	10.37	4.3	28	47	75	1.24	8.29	2.6
Chilopoda	12	1	13	11.32	2.22	8.61	1.74	0.37	1.4	15	1	16	0.66	0.18	0.56
Lacertilia	11	0	11	10.38	0.00	7.28	1.60	0.00	1.2	12	0	12	0.53	0.00	0.42
Other Coleoptera*	10	13	23	9.43	28.89	15.2	1.45	4.81	2.4	11	14	25	0.49	2.47	0.88
Diptera	9	8	17	8.49	17.78	11.3	1.31	2.96	1.8	12	11	23	0.53	1.94	0.8
Gastropoda	9	0	9	8.49	0.00	5.96	1.31	0.00	0.9	10	0	10	0.44	0.00	0.35
Insect larvae/pupa	6	1	7	5.66	2.22	4.64	0.87	0.37	0.7	6	4	10	0.26	0.71	0.35
Acarina	4	0	4	3.77	0.00	2.65	0.58	0.00	0.4	5	0	5	0.22	0.00	0.18
Thysanura	3	1	4	2.83	2.22	2.65	0.44	0.37	0.4	3	1	4	0.13	0.18	0.14
Angiospermae	3	0	3	2.83	0.00	1.99	0.44	0.00	0.3	na	na	na	0.00	0.00	0
Decapoda	3	0	3	2.83	0.00	1.99	0.44	0.00	0.3	3	0	3	0.13	0.00	0.1
Musci	2	0	2	1.89	0.00	1.32	0.29	0.00	0.21	na	na	na	0.00	0.00	0
Annelida, undet.	2	0	2	1.89	0.00	1.32	0.29	0.00	0.21	2	0	2	0.09	0.00	0.07
Lepidoptera adults	2	0	2	1.89	0.00	1.32	0.29	0.00	0.21	2	0	2	0.09	0.00	0.07
Lepidoptera larva	2	0	2	1.89	0.00	1.32	0.29	0.00	0.21	2	0	2	0.09	0.00	0.07
Other arachnida	2	0	2	1.89	0.00	1.32	0.29	0.00	0.21	4	0	4	0.18	0.00	0.14
Pseudoscorpionida	2	7	9	1.89	15.56	5.96	0.29	2.59	0.94	2	9	11	0.09	1.59	0.39
Carabidae larvae	1	1	2	0.94	2.22	1.32	0.15	0.37	0.21	2	1	3	0.09	0.18	0.11
Hirudinea	1	0	1	0.94	0.00	0.66	0.15	0.00	0.1	1	0	1	0.04	0.00	0.035
Nematoda	1	0	1	0.94	0.00	0.66	0.15	0.00	0.1	1	0	1	0.04	0.00	0.035
Apidae	1	0	1	0.94	0.00	0.66	0.15	0.00	0.1	1	0	1	0.04	0.00	0.035
Homoptera	0	1	1	0.00	2.22	0.66	0.00	0.37	0.1	0	1	1	0.00	0.18	0.035
Insecta, indet.	89	25	114	83.96	55.56	75.7	12.92	9.26	11.9	396	47	443	17.48	8.29	15.6
arthropod, unid.	19	0	19	17.92	0.00	12.6	2.76	0.00	1.98	46	0	46	2.03	0.00	1.62

na =not applicable

* includes eight families of Coleoptera

Comparison of nestling diet in the Kambui Hills and WAPF as determined by faecal analysis

The diet composition of nestlings in the Kambui Hills and the WAPF are compared in Table 5.1. The wide imbalance in sample sizes from the two areas would undermine the validity of statistical tests of association to compare the frequencies and proportions of individual taxa at the two sites. There is also a potential problem of pseudoreplication in comparing pooled frequency distributions of prey items from multiple faecal samples (Hurlbert, 1984). This is more likely with data from the Kambui Hills where several samples were sometimes collected on the same day below the same nest. In the more accessible WAPF, pseudoreplication was probably less of a potential problem. However, statistical tests of association have conservatively not been applied to the pooled data from both sites.

There was good agreement between percentage prey occurrence in nestling diet in the Kambui Hills and the WAPF (Spearman's rank correlation: $r_s = 0.726$, $p < 0.001$; $n = 34$). However, the number of prey categories recognized in the diet of Kambui Hills nestlings (34) was almost twice the number recognized in the WAPF (20). Lizards and snails which occurred in 10% and 8.5% of samples in the Kambui Hills respectively and formed 1.6% and 1.3% of prey occcurrence at this site were absent from the diet of nestlings in the WAPF. Also, with the exception of Carabid larvae and Homoptera (cicadas), all prey taxa which occurred in less than 2.5% of the total number of samples examined were absent from the WAPF samples (Table 5.1). On the other hand, the nine prey types identified as the main components of overall nestling diet in terms of numerical frequency (beetles, earthworms, termites, ants, spiders, crickets and grasshoppers, frogs, millipedes and earwigs) were present in nestling diet at both sites. This comparison suggests that the higher prey type diversity in the Kambui Hills nestling diet in comparison to the WAPF is probably a function of sample size and the degree of rarity of some prey types in nestling diet.

Five prey taxa (beetles, crickets and grasshoppers, Diptera, millipedes and pseudoscorpions) occurred in the WAPF samples in proportions which exceeded the

proportions in which they occurred in the Kambui Hills by a factor of two or more (Table 5.1). All other prey taxa which were common to the diet of nestlings in the two areas occurred either in comparable proportions at the two sites or in higher proportions in the Kambui Hills ie the site at which sample size was greater.

Nestling diet from direct observations

A total of 445 *P. gymnocephalus* nestling prey meals were observed (n = 6 nestlings at three nests in the Kambui Hills) of which 240 (54%) were identified to some degree (Table 5.2). Earthworms (36%), frogs (8%), beetles (6%), crickets (6%) and millipedes (5%) comprised the bulk of the identified prey meals. The 46% of prey meals that were unidentified were almost certainly small insects. This means that insects probably formed about 70% of the total number of observed prey meals.

Prey type diversity as determined by direct observation (22 prey categories) was comparable to that obtained by analysis of faecal samples in the WAPF (20 prey categories) but much less than the 34 prey categories ascertained from faecal analysis in the Kambui Hills.

Rank order correlation between nestling diet composition as determined by direct observation and that obtained by faecal analysis (% prey occurrencies) was statistically significant (Spearman's rank correlation: $r_s = 0.44$, $p < 0.02$; $n = 34$). In the following paragraphs, I use the results of the two methods to examine the magnitude and direction of the likely bias which may have arisen by using each of the two methods by themselves to determine *gymnocephalus* nestling diet.

Almost 60% of the prey occurrences in the direct observation method could not be identified beyond the level of class (Table 5.2). This compares to only 12% of the prey occurrences in faecal samples (Table 5.1). Although it is possible that some soft-

Table 5.2.The diet of *Picathartes gymnocephalus* nestlings determined by visual observation and presented as numbers and percentage of prey meals brought to the nest

Taxa	Prey occurrences: No.	% of identified meals	% of total no.of meals
Lumbricidae	86	35.80	19.33
Anura	19	7.90	4.27
Coleoptera	14	5.80	3.15
Diplopoda	13	5.40	2.92
Orthoptera	15	6.30	3.37
Scincidae	6	2.50	1.35
Formicidae	6	2.50	1.35
Aranaea	5	2.10	1.12
Blattidae	5	2.10	1.12
Chilopoda	1	0.40	0.45
Cicadas	2	0.80	0.45
Insect larvae	1	0.40	0.22
Lepidoptera larvae	1	0.40	0.22
Crabs	1	0.40	0.22
Snails	1	0.40	0.22
Odonata	1	0.40	0.22
Diptera	1	0.40	0.22
Unidentified insecta	59	24.48	13.23
Unidentified arthropod	3	1.24	0.67
Unidentified prey item	205		45.96

bodied prey were eaten by nestlings without leaving any trace in the faeces, the results of direct observation of prey meals and the data on the potential prey species present in the study area (Chapter 4), suggest that this is likely to be a very small proportion of the diet.

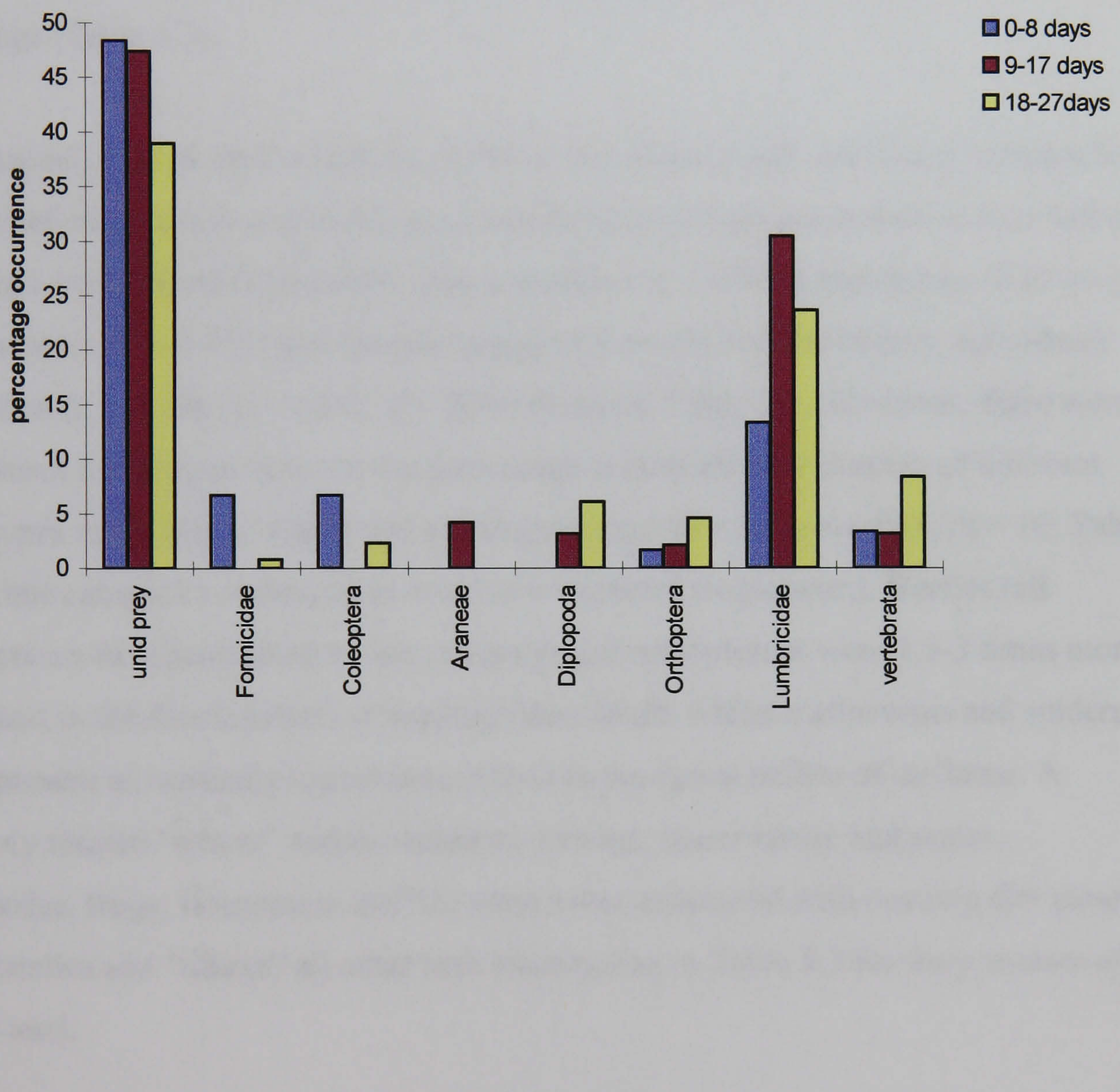
Two of the nine prey taxa identified as the most important constituents of *gymnocephalus* nestling diet from faecal analysis - termites and earwigs - were not observed being fed to nestlings (Tables 5.1 & 5.2). Whole specimens of these two taxa found in nestling faeces were usually less than 5mm in length. Most of the prey meals recorded as unidentified during direct observation were too small to be seen properly before being eaten by the nestlings.This suggests that a substantial proportion of prey which could not be identified visually may have been termites and earwigs.

The remains of reptiles in faecal samples could not be identified further than the ordinal level (Lacertilia). The lizards observed being fed to nestlings were all skinks. It seems likely that skinks were the main type of lizards in the diet of *gymnocephalus* nestlings.

Changes in diet with nestling age

The largest of the prey taxa - vertebrates, earthworms orthopterans and millipedes (see Table 5.5)- increased in proportion in the diet of nestlings as they grew older (Fig 5.1). The percentage occurrence of vertebrates (frogs and skinks) in the diet more than doubled from about 3% in the earlier stages of the nestling period to over 8% in nestlings more than 18 days old. Skinks were not seen being fed to nestlings till the last third of the nestling period. Conversely, there is some indication that adults fed their nestlings proportionately more of the smaller, presumably more easily digestible taxa during the earlier stages of nestling growth. As previously pointed out, unidentified prey were mainly prey items too small to be seen properly before being eaten (see also Table 5.5); the proportion of this category in the diet fell progressively through the three stages of the nestling period considered. Similarly, the proportion of

Fig 5.1. Percentage occurrence of main constituents of *Picathartes gymnocephalus* nestling diet at three stages of the nestling period. Percentage occurrence represents the proportion of the total samples in each period containing the category of the food in question. The taxa are arranged in ascending order of mean dry weight



ants and beetles, relatively small items in the diet, declined between the first and last third of the nestling period (Fig 5.1, Table 5.5).

Adult diet

Enough adult droppings were collected in the WAPF to allow comparison with nestling diet derived from faecal analysis (Table 5.3). There were 359 individual prey items identified in 31 adult faecal samples. The most striking difference between *gymnocephalus* adult and nestling diets was that vertebrates were absent from the diet of adults but formed one of the nine main constituent taxa of nestling diet (Tables 5.1 & 5.3). Also, only 14 prey categories were identified in adult diet as against 20 for nestlings (Table 5.3).

The ranked frequencies for each taxon in the diet were closely correlated between the faecal pellets of adults and nestlings in terms of percentage occurrence in the number of samples examined (Spearman's rank correlation $r_s = 0.878$); percentage of all prey occurrencies ($r_s = 0.941$) and the percentage of the total number of prey individuals identified ($r_s = 0.935$; $p < 0.001$, $n = 20$ in all cases; Table 5.3). However, there were significant differences between the percentage contribution by number of different prey types to the diet of adults and nestlings (G test: $G = 58$, $p < 0.001$, $df = 10$; Table 5.3, some categories coalesced to avoid low expected frequencies). Beetles (all coleopteran families treated as one category) and orthopterans were 1.5-3 times more abundant in the faecal pellets of nestlings than adults whilst earthworms and spiders were present in markedly higher proportions in the faecal pellets of the latter. A category termed "others" which contained earwigs, insect larvae and pupae, centipedes, frogs, Homoptera and Thysanura was associated with nestling diet (apart from beetles and “others” all other taxa remained as in Table 5.3 for the purposes of the G-test).

Table 5.3. Comparison of the diet of *Picathartes gymnocephalus* nestlings and adults in the WAPF, Sierra Leone

Taxa	Prey occurrencies:						Prey individuals:			
	No. of occurrencies		% of samples:		% of prey occurrences		No.of prey individuals		% of total no. of individuals	
	Adults	Nestlings	Adults (n=31)	Nestlings (n=45)	Adults (n=143)	Nestlings (n=270)	Adults	Nestlings	Adults (n=359)	Nestlings (n=567)
Lumbricidae	26	40	83.87	88.89	18.18	14.81	157	142	43.73	25.04
Formicidae	24	34	77.42	75.56	16.78	12.59	46	67	12.81	11.82
Isoptera	16	29	51.61	64.44	11.19	10.74	41	90	11.42	15.87
Carabidae adults	10	28	32.26	62.22	6.99	10.37	16	47	4.46	8.29
Insecta, indet.	12	25	38.71	55.56	8.39	9.26	20	47	5.57	8.29
Orthoptera	4	24	12.90	53.33	2.80	8.89	7	43	1.95	7.58
Diplopoda	15	19	48.39	42.22	10.50	7.04	15	24	4.18	4.23
Scarabidae	9	16	29.03	35.56	6.29	5.93	18	36	5.01	6.35
Araneae	10	14	32.26	31.11	6.99	5.19	18	16	5.01	2.82
Other Coleoptera*	6	13	91.35	28.89	4.20	4.81	8	14	2.23	2.47
Diptera	2	8	6.45	17.78	1.40	2.96	2	11	0.56	1.94
Pseudoscorpionida	5	7	16.13	15.56	3.50	2.59	5	9	1.39	1.59
Anura	0	3	0	6.67	0	1.11	0	4	0.00	0.71
Undet.Coleoptera	2	3	6.45	6.67	1.40	1.11	3	7	0.84	1.23
Dermaptera	2	2	6.45	4.44	1.40	0.74	3	2	0.84	0.35
Insect larvae/pupa	0	1	0.00	2.22	0.00	0.37	0	4	0.00	0.71
Chilopoda	0	1	0.00	2.22	0.00	0.37	0	1	0.00	0.18
Homoptera	0	1	0.00	2.22	0.00	0.37	0	1	0.00	0.18
Thysanura	0	1	0.00	2.22	0.00	0.37	0	1	0.00	0.18
Carabidae larvae	0	1	0.00	2.22	0.00	0.37	0	1	0.00	0.18
Total	143	270					359	567		

*See text for families included in this category

5.4.2. Prey size

Prey-size selection

Reconstructed dry weights of the main non-insect taxa in the visually determined diet of *Picathartes* nestlings, were calculated from the regression relationships between lengths and weights shown in Table 5.4. Similar information for insects and spiders was obtained from Rogers *et al* (1977).

The estimated lengths of prey in *Picathartes* nestling diet ranged from 1.0 mm (unidentified) -522.9mm (earthworm) but most prey (59%) were less than 2mm in length (Table 5.5). The mean estimated mass of nestling meals was 4.01g ± 0.55g (range: 5 x 10^{-4}g for an unidentified prey item to 59.9g for a frog; n = 266). However, 62% of prey items were less than 1g in weight (taxa which occurred only once in prey meal observations (Table 5.3) were excluded from this analysis).

It is possible that large "worms" (>300mm) were blind snakes (Typhlopidae) or burrowing lizards (Amphisbaenidae but such large items formed only a minute proportion (<1%) of this category. The recorded size range of unidentified prey is probably somewhat biased (underestimated), firstly because it was difficult to accurately estimate the sizes of these smaller prey and secondly because a general relationship between insect body length and biomass was used to estimate their sizes and this is known to be less accurate than taxon specific equations (Rogers *et al*, 1977; Calver and Wooller, 1982). Thirdly, some unidentified prey may not have been insects at all.

Table 5.4. Relationships between lengths (mm) and dry weights (g) (logx+1) of major non-insect taxa in the diet of *Picathartes gymnocephalus* nestlings

Taxon	Regression equation	r^2	n	p
Earthworms	y = -0.475+0.767	0.844	16	<0.001
Frogs	y = -0.180+0.924	0.947	7	<0.001
Millipedes	y = -0.061+0.163	0.906	10	<0.003
Lizards	y = 0.531+0.398	0.959	8	<0.001

An estimate of prey importance by weight

An estimate of the relative importance, by weight, of prey fed to *gymnocephalus* nestlings (n>1), was obtained by deriving weights for each individual food item seen delivered whole to the nestlings from their estimated lengths using regression equations shown in Table 5.4. and given by Rogers *et al* (1977) and Calver and Wooller (1982). Total biomass contribution of each prey taxon was determined by summing the derived weights for each item and the relative importance of the taxon assessed by simple proportion (Table 5.6).

Frogs contributed almost 50% of the total estimated biomass of the diet and were clearly the most important food resource for *gymnocephalus* nestlings. Earthworms accounted for 28% of the biomass and skinks for 8% so that more than 80% of the diet biomass was made up of non-insects. This is in strong contrast to the results from numerical frequency analysis, which suggest that *gymnocephalus* nestlings are mainly insectivorous with insects constituting about 70% of the diet (Section 5.4.1).

Table 5.5. The mean lengths (mm) and dry weights (g) ± se (n) of prey taxa fed to *Picathartes gymnocephalus* nestlings.

Taxa	Mean length (mm)	Range	Mean weight (g)	Range
Lumbricidae	44.5±9.87 (70)	4.2-522.9	4.5±0.78 (70)	0.17-39.8
Anura	58.5±7.55 (19)	16.6-132.8	27.6±3.35 (19)	8.35-59.9
Coleoptera	15.2±3.03 (13)	4.3-33.2	1.5±0.64 (13)	0.02-5.51
Diplopoda	28.0±4.9 (13)	8.3-66.4	0.47±0.04 (13)	0.25-0.73
Orthoptera	34.0±4.4 (14)	11-66.4	4.97±1.61 (14)	0.2-18.7
Lacertilia	61.9±16.9 (6)	16.6-132.8	18.9±1.89 (6)	9.6-23.8
Formicidae	7.8±1.95 (5)	2.7-10.96	0.05±0.021 (5)	0.02-0.09
Araneidae	32.9±17.3 (5)	8.3-99.6	2.91±2.46 (5)	0.22-12.8
Cicadas	52.6±13.8 (3)	24.9-66.4	20.1±16.04 (3)	2.12-29.9
Dictyoptera	21.1±1.87 (5)	16.6-24.9	0.06±0.0005(5)	$5\text{-}6\times10^{-4}$
Unid. Arth	16.6±3.26 (3)	11.0-22.2	$4.5\times10^{-3}\pm1.4\times10^{-3}$	$3\text{-}4.5\times10^{-4}$
Unid. insects	11.8±1.42 (51)	0.996-66.4	$3\times10^{-3}\pm3.7\times10^{-3}$	0.003-0.17
Unid prey	16.6±3.26 (3)	10.96-22.24	0.005±0.004(66)	0.0005-0.3

Table 5.6 Relative importance of food categories in the diet of *Picathartes gymnocephalus* nestlings, based on contribution by weight.

Taxa	No. of whole items brought to nest	Estimated total dry weight (g)	% of total biomass
Lumbricidae	70	317.3	28.6
Anura	19	523.5	47.3
Coleoptera	13	19.2	1.73
Orthoptera	14	69.64	6.28
Diplopoda	13	6.122	0.55
Scincidae	6	95.3	8.6
Formicidae	5	0.27	0.024
Araneae	5	14.6	1.32
Dictyoptera	5	0.029	0.0026
Cicadas	2	61.96	5.6
Unid. insects	59	0.165	0.015
Unid. arth.	3	0.0136	0.00123
Unid. prey	66	0.324	0.029

5.4.3. Comparison of diet composition and the catch composition of trap samples

Percentage similarity indices (*PS*) between nestling diet composition determined from faecal analysis in the Kambui Hills (Table 5.1) and the catch composition of pitfall traps (Table 4.1), visual surveys and a malaise trap (Table 4.3) are shown in Table 5.7. Pitfall trap samples and visual surveys showed 45-55% similarity to nestling diet composition and were more similar to nestling diet than malaise trap catches (by a factor of 2). The similarity between nestling diet and all trap catches was greatest when diet composition was determined as a percentage of total prey occurrencies.

Table 5.7. Percentage similarity indices between nestling diet composition and the composition of pitfall trap samples, visual surveys and malaise trap catches in the Kambui Hills, 1993.

	Pitfall trap samples	Visual surveys	Malaise trap catches
Nestling diet as % prey occurrencies	54.4%	54.5%	27.6%
Nestling diet as % of total no. of individuals	44.8%	49.2%	23.2%

Given the above results, data from malaise trap samples were not used in subsequent analysis of prey selection by breeding *gymnocephalus*; an analysis which involved comparing the percentage occurrencies of prey taxa in nestling diet with their relative abundance in the environment.

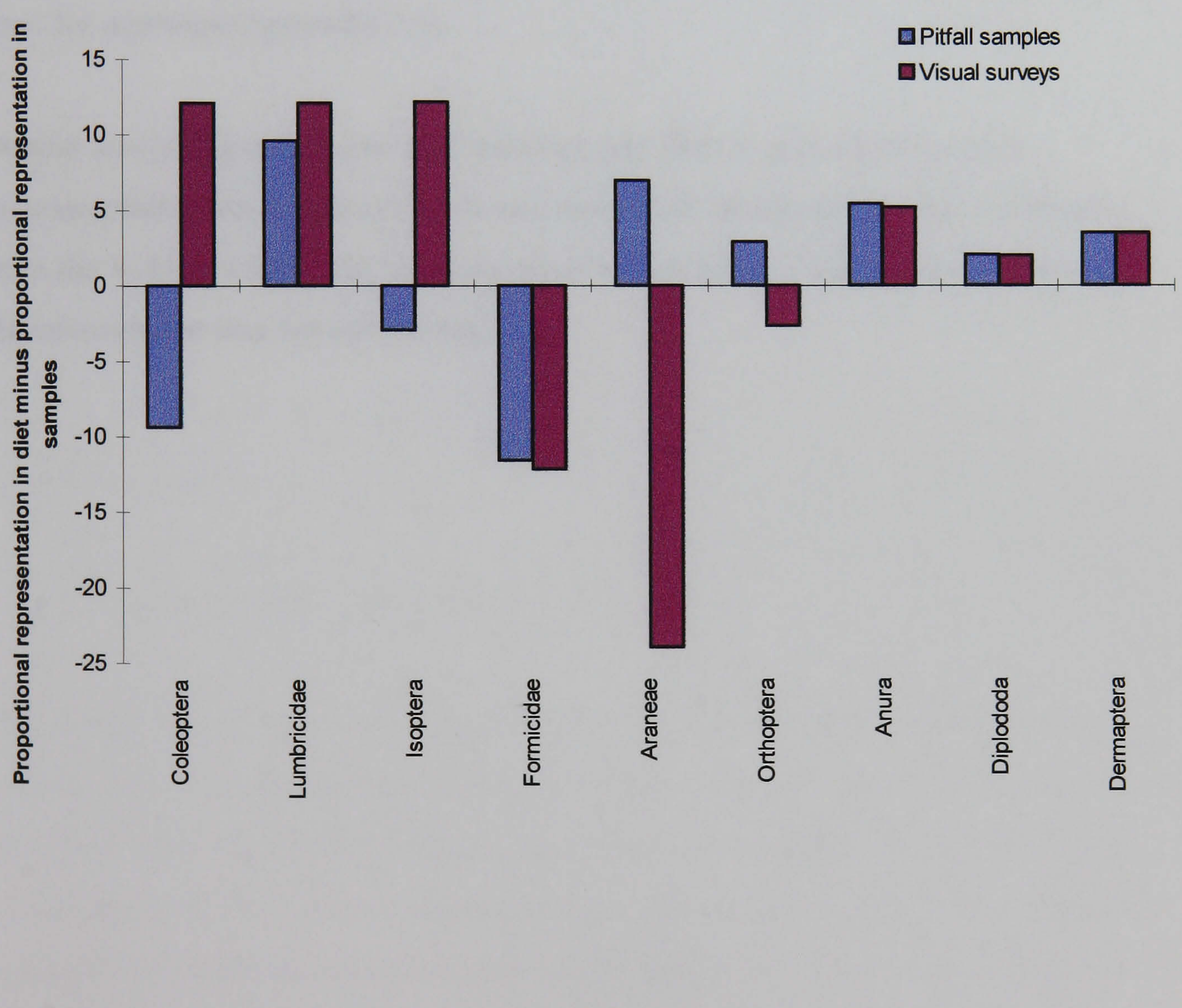
5.4.4. Prey selection

Because most sampling methods for fauna in the environment are selective, comparing nestling diet composition with trap catch composition does not provide valid information on whether birds select or avoid particular prey taxa in relation to their relative abundance in the environment (Cooper and Whitmore, 1990; Hutto, 1990; Wolda, 1990). However in the absence of an unselective trap/survey method, such comparison provided a way in which I could obtain some information on prey

selection by breeding *gymnocephalus*, provided trap bias could be clearly identified and monitored. To monitor the effect of trap bias on the analysis, I calculated a simple prey selection index (Strauss Index: Section 5.3.3) for each prey taxon in the diet of nestlings at the Kambui Hills study site using the results from both pitfall trap catches and visual surveys. The data for all prey taxa are given in Appendix 5.4 and shown graphically in Fig 5.2. for the major prey items in *gymnocephalus* diet. The results clearly show that trap bias influences whether a prey taxon would be considered as being actively selected or otherwise, if the results from only a single trap method alone were considered. For example, beetles have a negative prey selection index (avoidance) based on comparison with pitfall trap catches but a positive index (selection) based on visual surveys. The data are probably most reliable for taxa for which the indices derived from comparison with both sampling methods are in strong agreement (index > ±1). On these grounds, the results indicate that ants are underutilised in relation to the rates at which they were detected by sampling. On the other hand, earthworms, frogs, millipedes and earwigs were fed to nestlings in higher proportions than they occurred in traps/survey. Also, some relatively rare items in the diet - centipedes, crabs, lizards and pseudoscorpions - were taken in higher proportions than they occurred in trapping and survey samples (Appendix 5.4). The two sampling methods produced contrasting "pictures" for termites and beetles (underutilization based on pitfall trap catches and positive selection based on visual surveys). On balance, Orthoptera seem to have been used in the proportion in which they were detected in the environment (Fig 5.2).

The average rank difference between the ranks of the main prey taxa in *gymnocephalus* nestling diet (> 3% of prey occurrencies) and their corresponding ranks in pitfall trap catches and visual surveys are shown in Table 5.8. (data for all prey taxa are given in Appendix 5.5. The average rank difference for the two sampling methods is used as an index of relative preference for all the prey taxa in the diet (Krebs 1989). The results show that earwigs are the most preferred food resource in *gymnocephalus* nestling diet, although they constitute only 3.5% of total prey occurrencies in the diet (Tables 5.1 & 5.8 and Appendix 5.5).

Fig. 5.2. Comparison of diet to prey abundance in survey samples for major prey items in the diet of *Picathartes gymnocephalus* nestlings. Bars above and below the mid-line represent prey categories selected or avoided respectively



In contrast, termites and ants which are the first (12.2%) and third (11.2%) most frequently occurring items in nestling diet in the Kambui Hills are the least preferred of the main food items in the diet (Tables 5.1 & 5.8). They were also lower in rank preference than relatively rare items in the diet such as crabs (0.44% prey occurrence), pseudoscorpions (0.29% prey occurrence) and lizards (1.6% prey occurrence; Appendix 5.5). The rank preference analysis suggests that of the nine main prey taxa in the diet in terms of numerical frequency of occurrence, earthworms, beetles and frogs are the most preferred food resources after earwigs. This agrees to some extent with the numerical frequency results (Tables 5.1 & 5.2).

These results support the prey selection analysis (Fig 5.2), which suggests that ants are underutilised and that crabs, lizards and pseudoscorpions are actively selected as food for nestlings (Appendix 5.4).

Similar analysis to investigate prey selection and dietary preference by adult *gymnocephalus* was not possible because most adult faecal samples were collected from the WAPF, a study site at which relative abundance of ground storey fauna in the environment was not carried out.

Table 5.8. Preference rank order for main prey items in *Picathartes gymnocephalus* nestling diet. Taxa arranged in decreasing order of preference.

Prey taxa	Differences in rank between different prey taxa in nestling diet and their abundance in trap/survey samples			
	Pitfall traps	Visual surveys	Average rank difference	% prey occurrences
Dermaptera	-21	-22	-21.5	3.5
Lumbricidae	-2.5	-14	-8.25	12.2
Coleoptera	0	-15.5	-7.75	12.2
Anura	-4	-3	-3.5	6.4
Diplopoda	0	1	0.5	3.3
Orthoptera	-0.5	3	1.25	4.2
Araneae	-2.5	5	1.25	8.3
Isoptera	-0.5	3.5	1.5	12.2
Formicidae	4	3	3.5	11.2

5.5. DISCUSSION

5.5.1. Assumptions in the methodology

Faecal analysis has been widely used in dietary studies of insectivorous birds (eg. Davies, 1977a & b; Greig-Smith & Quicke 1983; Rolando & Laiolo, 1997) but the question of the extent of bias introduced by differential digestion of hard- and soft-bodied prey remains pertinent to any analysis of the results (Ormerod, 1985). Hard-bodied items which are harder to digest may be proportionately over-represented in droppings. However, with careful analysis of droppings, a good knowledge of the particular fragments representing each food type and of the potential prey base in the study area, diet "indicators" are not lost in a differential fashion as digestion proceeds (Tatner, 1983). There is usually a close correspondence between faecal and stomach

samples (Rosenberg and Cooper, 1990) and droppings do not reflect a bias against small or soft-bodied prey items (Ralph *et al*, 1985). Also, such bias would not explain dietary differences recorded between adults and nestlings and between nestlings of different ages (Section 5.4.1). In this study, simultaneous use of direct observation with faecal analysis, and year-round pitfall trapping in the study area meant that potential soft-bodied prey likely to turn up in the faeces were known in advance and a special effort could be made to detect them and so minimize bias (see Section 5.3.1.). Consequently, I felt that I could detect hard-bodied prey, such as beetles, and the hard fragments of soft-bodied prey, such as earthworm chaetae and spider fangs equally well. This supports a similar impression obtained by Chapman and Rosenberg (1991).

The fragmented state of prey remains in droppings is another drawback of faecal analysis. This may inhibit recognition and enumeration of prey remains and distort the results of diet analysis, in particular, the proportion of identified prey individuals. In this study, all frequently encountered prey taxa (>3% prey occurrences) were fairly easily recognised and scored. An exception was earthworms, whose chaetae were easily spotted at x100 magnification but which could not be easily scored in terms of number of worms eaten. A conversion factor to determine the relation between the number of earthworms fed to captive birds and the number of chaetae voided has been previously used to address this problem (see Section 5.3.1.). However, the time between ingestion and voiding of the last chaetae is often long (up to 10 hours), so that chaetae from the same worm appear in several faecal samples (Galbraith 1989; M. Ausden, pers. comm.). Also, the number of segments and, therefore, chaetae per earthworm is usually highly variable. This has meant that conversion factors for earthworms are often inaccurate (Galbraith, 1989). However, the proportion of earthworms obtained here from faecal analysis using the assumption that 10 chaetae equalled one earthworm eaten (36%, Table 5.1) was the same as the corresponding proportion obtained by direct observation (Table 5.2).

The main drawback of direct observation was the high proportion of prey meals that could not be identified (Table 5.2). Prey size analysis (Table 5.5) and the results of

the faecal sample anlysis (Table 5.1) suggest that these unidentified prey items were probably small insects.

5.5.2. The Diet

Diet composition

In terms of prey diversity and numerical abundance, the diet of *Picathartes gymnocephalus* nestlings is dominated by invertebrates, with insects forming the major component (Table 5.1). Beetles, earthworms, termites, ants, spiders and crickets were the most numerically significant taxa (Tables 5.1 & 5.3). However, frogs and lizards contributed most of the food biomass (Table 5.6), even though vertebrate occurrence in the diet was relatively low (5-6%; Tables 5.1 & 5.2). Earthworms were both numerically and gravimetrically important, occurring in almost 90% of faecal samples (Table 5.1) and contributing 29% of the biomass of prey meals identified by direct observation (Table 5.6).

Adults had a broadly similar diet to nestlings but adult diet was apparently less varied than nestling diet; six prey categories identified in nestling diet were not detected in adult diet (Table 5.3).

Previous workers have noted the apparent insectivorous nature of *Picathartes* diet. Stomach analyses by Sharpe and Bates (1908), Lowe (1938) and Walker (1939), and direct observation by Tye (1987) all found insects to be the main numerical constituents of *Picathartes* diet with Orthoptera (Blattidae, Tettigonidae), Dermaptera (Forficulidae), Coleoptera (Elateridae, Anthribidae, Curculionidae, Staphylinidae), Hymenoptera (Formicidae-*Dorylus* ants) and Lepidoptera cited as insect prey taxa. This basically agrees with the results of this study except that Isoptera (termites) which were the most frequently occurring insect prey in nestling faecal samples in this study (Table 5.1) were not recorded in previous analyses. Termites occur in local, irregularly distributed super-abundant clumps (pers. obs.) and they may not have occurred in the small sample sizes in previous investigations ($n < 3$ in all cases).

However, Bannerman (1951) and Glanville (1954) noted that adults in captivity were fed on termites among other food items and J.S. Sawyerr (1965 *in litt* to Grimes) stated that the main food included termites.

The importance of earthworms and vertebrates in providing most of the biomass of the food of *Picathartes* has not been previously recognized.The early *Picathartes* stomach analyses did not record any earthworms (Sharpe and Bates, 1908; Lowe, 1938; Walker, 1939) but Glanville (1954) noted that captive birds were fed on worms, while Grimes (1963) saw food resembling worms, about 80mm long, fed to *gymnocephalus* nestlings. Tye (1987) provided the first definite records of *Picathartes* nestlings being fed worms in the wild and noted that these were the largest items in their diet. Here, the high importance of worms in the diet of both nestlings and adults (Table 5.3) suggest that they were taken regularly and were apparently easier to obtain than vertebrates. Although there are no data, this could mean that earthworms are the most energetically efficent food item in *Picathartes* diet, providing the greatest yield for the least energy expenditure (Tables 5.5 & 5.6).

The low frequency of occurrence of frogs and lizards in *gymnocephalus* nestling diet (<5% frequency of occurrence; Tables 5.1 and 5.2), means that taking into account the time spent collecting earthworms (<20% frequency of occurrence; Tables 5.1 and 5.2), then *gymnocephalus* parents spent about 75% of their time collecting large numbers of insects and other invertebrates which contributed only about 20% of the biomass of the diet. This suggests that they may be unable to obtain a regular supply of vertebrates more easily and therefore take them opportunistically.

Frogs (Lowe, 1938; Glanville, 1954; Sawyerr, 1965; Tye, 1987) and lizards (Fotso 1993) have been previously noted in the diet of adult and nestling *Picathartes*. Here, I failed to find vertebrates in the diet of adults, although they occurred in the diet of the nestlings (Table 5.3). This could have been an artefact of my sample ie adults were feeding on vertebrates but vertebrate remains did not occur in the samples I examined. This is unlikely, since previous records are based on either single stomach analysis (Lowe, 1938) or casual observations (Sawyerr 1965, Fotso 1993) whilst 32 droppings

collected over three months were examined here. A more likely explanation is that adults did not feed on vertebrates during the nestling period, when my samples were collected, but may have fed on them outside the breeding season. If earlier records were taken outside the breeding season, this would account for the discrepancy. This explanation would fit in with previously described size-related differences in other bird species between the diets of adults and their nestlings, with larger prey being fed to the latter (e.g. Royama, 1970; Davies, 1977b; Ormerod, 1985). If vertebrates were not very easy to obtain and yet could provide a large amount of biomass in a single meal, parents would optimise nestling food provisioning rates by feeding all vertebrates found to nestlings. Foraging efficiency is known to be optimised in several species, in some instances whilst feeding young (eg Krebs *et al*, 1977; Carlson, 1983). These results suggest this may well include *Picathartes*.

Picathartes nestlings were fed larger prey as they grew older (Fig 5.1). Most notably, lizards were only fed to nestlings when they were over two weeks old. Similar dietary change with nestling age has been previously recorded in various bird species (eg Bibby, 1979) and this has been attributed to (a) age-related changes in nutritional requirements (Royama, 1970), (b) gape size and prey availability (Davies, 1977a) and (c) a response to the increasing gross energy requirements of nestlings (Ormerod, 1985). Food provisioning rates by *gymnocephalus* adults depend on brood size and are significantly correlated with nestling age (Section 3.5.3.: Food provisioning). This indicates that *gymnocephalus* adults, like many other bird species (eg see Galbraith 1983), respond to changing energetic requirements of their brood by adjusting the rate of feeding. An additional tool for adjusting the energetic intake of nestlings would be by progressively changing the sizes of food items brought to the nest as described in this study. This has also been noted in other species (eg Ormerod 1985) and is the only hypothesis for which there is some evidence (albeit indirect) from this study. More data would be required for more definite conclusions

Foraging microhabitat

Most of the food items in the diet of *Picathartes gymnocephalus* adults and nestlings (eg ground beetles, ants, earthworms etc; Tables 5.1 and 5.3) confirmed preliminary observations that the birds foraged mainly on the forest floor and in low undergrowth. Nestling diet in terms of percentage prey occurrence showed 55% similarity with pitfall catch composition and visual surveys (primarily monitored organisms on or close to the forest floor) but only 28% similarity to malaise trap catches (which caught flying insects and leaping insects)(Table 5.7.). This supports the suggestion that *Picathartes* foraged mainly on the soil surface.

However, crabs (Decapoda) occurred in a small proportion of the birds droppings (Table 5.1 & 5.3) but were absent from the traps and surveys used to monitor faunal abundance in the terrestrial environment. Casual observations indicated that crabs occurred mainly in streams in the study area. This suggests that *Picathartes* occassionally foraged in these streams.

There were some conspicuous species in the study area which were not prominent in either the birds' diet or the trap/survey samples. These were Lepidoptera adults and caterpillars and cicadas (Homoptera). Butterflies were usually seen outside the transect band within which they could have been counted on visual censuses; probably because of their relatively high sensitivity to disturbance and capability of rapid movement. Thus, although they formed 16% of malaise trap catches, they did not feature at all in visual censuses (Chapter 4: Table 4.3). *Picathartes* would also have found it difficult to catch them, thus accounting for their low frequency of occurrence in the diet (0.21% prey occurrence; Tables 5.1-5.3). Caterpillars were most often seen on foliage and may have mainly occurred outside the foraging niche of *gymnocephalus* adults which were not seen gleaning leaves. Cicadas were heard continually on visual censuses suggesting a high density of occurrence in the study area but they were rarely seen (0% frequency occurrence in censuses). Cicadas were larger than any other insect prey identified as nestling prey meals (Table 5.5). If *P. gymnocephalus* parents try to optimise feeding efficiency when provisioning

nestlings, cicadas should make attractive prey. Low frequency of occurrence in the diet (0.8%; Table 5.2) may indicate that, like vertebrates, they were relatively hard to obtain. This may have been because of their camouflage or because *Picathartes* usually forages at heights of less than 0.5m from the soil surface.

Resource use in relation to prey abundance

There was significant correlation in rank abundance between the invertebrate categories in the nestling diet and the composition of pitfall trap samples and visual census results (Section 5.4.3). Ants, beetles and termites which formed 60% of the total pitfall trap catch each occurred in over 70% of nestling droppings (Table 5.1) and were three of the six most important constituents of nestling diet in numerical terms (Section 5.4.1). The occurrence of ant columns and termite concentrations in visual surveys peaked in January and February (Chapter 4: Fig 4.6d). Increased abundance of beetles and termites were mainly responsible for elevated biomass levels of pitfall trap samples observed between November and December (termites) and January and February (beetles). *Picathartes gymnocephalus* laid eggs between June and December with peak numbers occurring in October (Fig.4.8). Chicks were in the nest from August to January with highest numbers being found in November (Fig 4.8). This suggests that the young were fed on insect taxa which reach their seasonal peak when most young were either in the nest or were dispersing fledglings still dependent on their parents for food. This is in agreement with the hypothesis put forward in Chapter Four (Section 4.6.2) that finding food for dispersing fledglings is probably an energetically limiting stage in the annual cycle of *gymnocephalus*.

Earthworms and vertebrates were the most important constituents in terms of biomass in nestling diet (Table 5.6). The occurrence of frogs and lizards in trap/survey samples did not show any seasonal pattern, perhaps because too few were detected (Appendix 4.5). Visual sampling should favour detection of these relatively large organisms. Their relatively low detection rates by my sampling methods suggest a relatively low density of occurrence in the study area, which would be expected from their trophic niche (secondary consumers) relative to the other important constituents of nestling

diet (mainly primary consumers and detritivores). This would explain their relatively low frequency of occurrence in the diet and support the suggestion that they may be relatively difficult to obtain and are taken opportunistically by *gymnocephalus*.

Earthworms were also detected at relatively low rates by my sampling methods (Appendices 4.2 & 4.3), probably because they require specialized sampling techniques which I did not use (see Ausden, 1996). However, unpublished studies by Okoni-Williams (1995) in the WAPF indicate that earthworms were easier to detect by sampling during the wet season in Sierra Leone (May to October) than at other times of the year. The soil would be softer during the rains and earthworms easier to extract. Worms are also more likely to be closer to the soil surface in the wet than in the dry season, since they would tend to avoid dessication during the latter period by burrowing deeper. These factors are likely to make it easier for *Picathartes* to capture earthworms during the wet season, a period when they may be feeding nestlings. However, earthworms were present in significantly higher proportions in the diet of adults than nestlings (Table 5.3). This could be because adults were using worms as their main high biomass food items if they had suspended feeding on vertebrates as postulated here.

Prey Selection

Because of the selective nature of the trap/survey methods I used to measure prey abundance in the environment, it is difficult to determine from the data collected whether *gymnocephalus* select certain types of prey, or merely collect them in proportion to their availability. Assuming that dietary analysis in this study was largely correct, then the accuracy of the prey selection index used to provide some measure of the degree of prey selection by *gymnocephalus* (Fig 5.2) depended on how well my sampling methods could detect the various prey taxa in the environment. If a particular prey taxon was actually quite abundant in the environment but could not be detected by my sampling methods except at erroneously low levels, this would tend to result in a false positive selection index for that prey taxon. Since sampling was directed at the microhabitat in which *gymnocephalus* usually forage, the reverse

scenario is hardly likely ie a false negative selection index deriving from erroneously high prey detection levels in the environment.

On the above grounds, the inference from the data that *gymnocephalus* avoid or underutilise ants in relation to their abundance in the environment would seem to be justified (Fig 5.2). *Picathartes* is known to follow swarms of carnivorous doryline ants but, like many other ant-following bird species, this is mainly to capture prey flushed by the ants (Willis and Oniki, 1978; Willis, 1983). Willis and Oniki (1978) have further pointed out that few worker ants of any species are bird food. In this study, ants of various families occurred in both nestling and adult diets of *gymnocephalus* at relatively high levels (Tables 5.1 & 5.3; Fig 5.1). This has also been reported by Tye (1987). However, only 6% of 111 ant occurrencies in nestling diet were doryline ants, suggesting that the birds rarely use these ants to feed their young. Ants may have been a readily available source of food in the study area but were unattractive prey to *gymnocephalus* (Table 5.8) perhaps because of their relatively small size (Table 5.5) and the physical and chemical defences some species possess. Chapman and Rosenberg (1991) and Chesser (1995) noted similar underutilization of ants as food for nine species of obligate ant-followers in the Amazon basin.

Of the main numerical items in its determined diet, *Picathartes gymnocephalus* actively selected earthworms, frogs, millipedes and earwigs as prey for nestlings (Fig 5.2). This inference is most likely to be unreliable for those taxa for which my sampling methods were unsuitable or inaccurate. Earthworms, earwigs and millipedes could probably have been more accurately sampled by litter sampling or in the case of earthworms using Potassium Permanganate solution (Ausden, 1996). This may have yielded higher environmental abundance levels and correspondingly depressed the positive prey selection index (Fig 5.2) and rank preference index (Table 5.8) obtained. However, although fairly cyptic, it is difficult to see how frogs available to *gymnocephalus,* ie not under stones or in cracks and crevices, could have been sampled more accurately. I therefore suggest that frogs are indeed actively selected as prey for *gymnocephalus* nestlings as the data indicate. This is almost certainly because

of the substantial advantage that accrues from feeding on frogs (and lizards), in terms of increasing the biomass of the nestling diet (Table 5.6.) and providing the energetic requirements of the nestlings.

In conclusion, these results suggest that *Picathartes gymnocephalus* feeds its nestlings on a fairly diverse, generalized diet but probably obtains its prey using specialized foraging behaviour. Sherry (1990) has argued that foraging specialization may result in stereotyped, but not necessarily narrow diets. This is certainly the case for *Picathartes*.

The ability of *Picathartes* nestlings to be reared on a wide variety of prey would confer a high degree of adaptability as birds would be able to exploit different prey items if preferred food became scarce or unavailable. An unspecialized diet is also often associated with widespread distribution and rapid colonization of new environments. This suggests that the restricted range of the genus and the apparently small size of the populations of the species are not related to its ability to find food.

CHAPTER SIX

ABUNDANCE, DISTRIBUTION AND HABITAT

6.1. AIMS

The research described in this chapter aimed to:

a) determine the distribution of *gymnocephalus* throughout Sierra Leone

b) determine quantitative ecological parameters for the habitat requirements of *gymnocephalus*

c) investigate the relation between bird distribution and topography.

d) estimate population density of *gymnocephalus* in a selected forest in Sierra Leone

6.2. PREVIOUS WORK

Picathartes gymnocephalus is frequently described as local and uncommon (see review in Collar and Stuart, 1985; Collar *et al*, 1994) but there are no available data on populations. There have not been any previous surveys to determine the species' distribution and abundance anywhere in its range. Present information comes mainly from individual sightings and collections obtained in the course of other work (see Chapter One).

King (1979) guessed the known *gymnocephalus* population in Ghana to be 200- 300 pairs. There has not been any other attempt to put a figure on the species' population size in any country.

More information is available for *oreas*. Ash (1991) conducted a search for *oreas* in key forest sites in southeastern Nigeria and found 91 breeding sites.This was thought to reflect a total population of about 500-1000 birds in an area of about 900 km^2 of forest. I do not know of any other population estimates derived from systematic surveys for *oreas* anywhere else in its range.

In general, quantitative population data on Afrotropical birds are scanty and such research has only recently begun (Dowsett 1985; Dowsett-Lemaire, 1989; Pomeroy, 1992; Jones *et al*, 1996). There is more information on African birds' distribution but many references merely list species locations (eg Moreau, 1966; Hall & Moreau, 1970; ICBP, 1992). Analyses which relate bird distributions to habitat variables are much fewer and are only presently emerging (eg.Osborne and Tigar, 1992; Harrison & Martinez, 1995; Lens *et al,* in press). There are indications in this emerging body of work that some of the standard bird census techniques developed and widely used in temperate regions (e.g. Bibby *et al*, 1992) are not directly transferable to some habitats (eg rain forest) and species in Africa. There is therefore a clear need for further research on the distribution and abundance of Afrotropical birds as well as on the development of appropriate census methodology (see Burgess *et al*, 1997).

This chapter presents results of the first formal attempt to ascertain the distribution and numbers of *gymnocephalus* anywhere within its range. This work should make the status of the species clearer and provide information which can be used in its conservation. It should also provide insights into appropriate census methodology for a secretive African bird species and extend our knowledge of a threatened Afrotropical taxon.

6.3. METHODS

6.3.1 Survey work

Surveys were carried out on two different spatial scales:

a) an extensive country-wide survey to collect information on overall habitat preferences, distribution and conservation status.

b) an intensive survey focussed on one forest (WAPF) to determine *gymnocephalus* population density and to collect detailed information on distribution patterns.

The extensive survey

Site selection

Of the 29 forest reserves in Sierra Leone, 10 were selected to be searched for *P. gymnocephalus*, on the basis of the following criteria:

a. size: the first 10 largest reserves which fitted the other criteria, were selected for the survey. Together, these reserves constituted 86% of the total forest reserve estate in Sierra Leone

b. geographical location and access: selected reserves had to be accessible from Freetown such that surveys could be completed within two to three weeks.

c. previous reports of *gymnocephalus* in an area: reserves in which *gymnocephalus* had been previously reported were given priority in selection.

Three of the ten selected reserves were eventually not surveyed because of concerns about security.

Choice of survey method and likely biases

From previous work in the Gola forest in which I participated (Allport *et al*, 1989), as well as from work elsewhere (Ash 1991), I knew that local villagers, especially hunters and trappers, often had good knowledge of the locations of nesting sites of *Picathartes*. I therefore decided to carry out the extensive survey by canvassing villages in close proximity to the targeted reserves and asking knowledgeable local people to direct us to breeding colonies they knew about. This method had some obvious biases but it was the quickest and probably the only feasible way of carrying out a survey of this nature. Ample proof of this comes from Allport *et al* (1989), in which conventional census techniques such as cold searching, calling bird surveys and mist-netting did not yield any *Picathartes* records in two months, but over 20 breeding colonies were found in the succeeding two months using local knowledge.

It was recognized that local knowledge of nesting sites was likely to be biased towards those colonies closest to areas of human activity and away from colonies close to the

centre of reserves and/or in especially inaccessible terrain. However, a point was made to seek out individuals known to regularly go a long way into the forest reserves.

Survey team

The survey team usually comprised the following: the author; Ali Koroma, a graduate zoologist from the University of Sierra Leone (see Section 2.3), one or more field assistants and a local guide who could speak the local language.

Selection of villages for survey work

Villages around the boundary of a reserve were visited in order of ease of accessibility, but priority was given to villages closest to the reserve boundaries and an effort was made to visit some villages on all sides of the reserve.

In the Gola forest and Kambui Hills, there were too many villages around the forest reserves to be visited by the survey team within the time available for surveys. Instead, one member of the team, A.L. Macfoy, toured as many villages as possible prior to visits by the survey team and identified those villages where *gymnocephalus* was familiar to people. This reduced the number of villages which the whole team needed to visit.

Survey implementation

At each village, an initial meeting was held with the chief and his council of elders to brief them on the purposes of the survey team's visit and to enlist their help in obtaining information. Further meetings (formal and informal) were then held with villagers. Coloured pictures of *gymnocephalus* and its nest sites were used to determine whether people knew the bird and/or its nesting sites. People who indicated they had such information were questioned further using a structured questionnaire (Appendix 6.1.). Respondents who we thought had genuine information were then asked to guide members of the survey team to *P.gymnocephalus* nesting sites for a

small fee. At each nesting site, habitat and site characteritics were measured as described in Section 6.3.2. below.

All sites were plotted on standard 1:50,000 maps of the area concerned obtained from the Ministry of Lands. Grid references were derived from the 1000m^2 Universal Transverse Mercator (UTM) Grid Zone and grid references given to the nearest 100m. Letters in front of the numbered grid references (eg Appendix 6.3) enabled 100,000m^2 identification. Site positions were determined by taking compass bearings to the nearest village, estimating the distance from that village and comparing topography on the maps with physical landforms encountered on the way to the site.

The intensive survey

The main aim here was to estimate the population density of *P. gymnocephalus* in a selected forest reserve. The WAPF was well suited for this purpose because of its close proximity to Freetown where the author was based and the comparatively good security in the area.

A 1:50,000 map of the WAPF reserve was divided into 23 numbered 2.5 x 2.5 km blocks covering the whole reserve. Fifteen of these blocks were randomly selected (lucky dip method). Each selected block was searched for *gymnocephalus* breeding sites for 2 - 3 days between January and September 1996. An attempt was made to keep search effort constant by searching areas with difficult terrain for one extra day than other areas, when this was thought necessary. Some areas which had been previously searched during the extensive survey coincided with this later census. Search effort in such blocks were reduced to take account of the previous search time in the area and the results of both censuses combined. The total area covered by the searched blocks (93.8 km^2) represents 53% of the total land area of the reserve.

Typically, the field assistant (Tamba Fatoma - a forest ranger familiar with the area) would visit each block in advance of the formal survey to find access paths and demarcate as best as possible the limits of the block. Two searchers then spent two to

three days (at least 14 man-hours) walking along stream courses and accessible paths within each block. A special effort was made to search the banks of all streams and rivers shown on maps of the area. The main problem with this method was determining that searches were kept within specified blocks, so that search overlap between blocks was minimised and, conversely, that large unsearched areas did not exist between blocks.

6.3.2 Habitat measurements

The circular sample plot method (James and Shugart, 1970) was used to collect habitat data at nesting sites. The habitat and nest site variables recorded for each nesting site are defined in Table 6.1. A nesting site was taken as a single discrete rock, cliff or cave, with one or more *gymnocephalus* nests which was spatially separated (> 5m) from any other such rock, cliff or cave. However, sites which were within about 50m radius of each other were considered to share the same set of habitat characteristics, except if this was visibly not the case.

Measurement of tree density and basal area

Tree density and basal area were measured by recording the number of trees within a 0.04 ha circle demarcated adjacent to each breeding colony (after James and Shugart, 1970). The circle of the required size was obtained by measuring 11.28 m on a piece of string and using the string to obtain this distance in five pentaradiate directions from a chosen central point. Brightly-coloured markers (usually yellow strips of cloth) were used to indicate the perimeter of the circle. Use of the string made measuring the required distance in difficult terrain much easier. Staying within the circle, the number and dbh of all trees as defined in Table 6.1 were recorded. Tree diameter was measured using a forester's diameter tape from which the diameter could be read off directly.

Table 6.1. Definitions of nest site characteristics and habitat variables measured at *Picathartes* nesting sites (see text for detailed methodology)

Variable	Definition (see text for fuller details)
Surrounding habitat features	
Tree density	No. of trees per ha where a tree is taken as a woody plant more than 9m in height and 10cm diameter at breast height (dbh).
Basal area	Basal area (m^2) of trees per ha, where the basal area of tree is the cross-sectional area at breast height.
Site slope	Angle of slope (from the horizontal) of the location of the nesting site .
Canopy cover	Percentage of the sky visible from the ground at each nesting site (see text)
Canopy height	Mean height (m) of trees in the main forest canopy.
Distance to stream	Shortest distance (m) to nearest water-course.
Distance to edge	Shortest distance (m) to nearest man-made clearing.
Nest site features	
Rock height	Height (m) of highest point on discrete rock bearing at least one *gymnocephalus* nest.
Rock face width	Width (m) of discrete rock face bearing at least one *gymnocephalus* nest. A discrete rock face was taken to be a plane surface of a rock at an angle of 45^{o} or more from any other adjacent plane surface.
Rock face bearing	Compass direction (degrees) of nest-bearing rock face.
Rock face slope	Angle of nest-bearing rock face from the vertical.
Inter-nest distance	Mean distance (cm) between complete nests on a discrete rock face.
Nest height above ground	Mean distance (m) above ground of base of all nests on a discrete rock . .

Estimates of total tree density per hectare were obtained by simply multiplying the number of trees in each circle by 25.

Tree basal area (a measure of woody biomass) was calculated for each individual tree by using half its dbh value in the mathematical formula for cross-sectional area (πr^2). Simple summation of individual tree basal areas and multiplication by 25 resulted in a value for tree basal area (m^2) per hectare around each breeding site.

Measurement of site slope

The slope of the site on which a breeding colony was situated was estimated using a disc clinometer. The mean of five such readings measured from five different positions, from 20m in front of the nesting rock was taken as the site slope.

Estimation of canopy cover -

Canopy cover was assessed as a percentage, through an ocular tube sighted directly overhead (James and Shugart, 1970). The ocular tube was made by tautly crossing two pieces of string at right angles to each other across one end of a toilet roll tube. By sighting directly overhead on alternate steps of two transects at right angles to one another across the 0.04 ha sample plot, 20 plus or minus readings were recorded for the presence or absence of canopy cover at the points where the threads of the ocular tube crossed (see also, Bibby *et al*, 1992). Canopy cover at each breeding site was then taken as the percentage of pluses recorded out of the total of 20 readings.

Measurement of canopy height.

Canopy height was measured with a hypsometer. At, or close to points at which canopy cover was recorded, the hypsometer was aimed at the top of a tree about 15 - 25m away in the main canopy. The height indicated on the hypsometer which corresponded to the estimated horizontal distance from the tree was read off directly. The mean of 20 such readings was taken as a measure of canopy height.

Measurement of rock slope

The slope of each nest-bearing face of a rock was measured using an improvised clinometer consisting of a protractor and a plumb-line (string with a small pebble tied at the end). Slope was usually measured at the edges of a rock-bearing face. The plumb-line indicated the vertical plane and the deviation of the rock face slope from this plane read off on the protractor. The mean of five readings was taken as the slope of the rock face.

Other measurements

Searches were made within a 500m radius of each breeding site for water-courses and clearings and the distances estimated by eye. Where no water-course was found, the distance to the closest water-course marked on a map of the area was used. In the case of clearings, only distances to those clearings noted on the way to the breeding site or found in a search round the site were used. Rock dimensions were taken using standard metric measuring tape.

General

The number of complete and incomplete nests on the face of the rock or cliff constituting a breeding site were recorded, as well as its compass bearing. Also, each site was carefully inspected for signs of recent use eg fresh/wet mud on nests; presence of faecal remains, feathers or egg shell pieces below nests and fresh lining in nests. Each site was then designated as active (ie currently or recently in use) or abandoned (no longer in use) on the basis of this inspection. Whether the site was located within the boundaries of a forest reserve or not was also recorded.

6.4. RESULTS

6.4.1. Survey coverage

Surveys for *Picathartes gymnocephalus* nesting sites were carried out in seven of the ten initially selected forest reserves between March 1990 and February 1994 (Table 6.2 and Fig. 6.1). Together, these seven reserves have a total area of 1589 km^2 (54% of the total forest reserve estate in Sierra Leone). A total of 126 days was spent in the field during which 108 villages were visited (Table 6.2). Coverage was biased to the east of the country because of the predominance of known suitable habitat (forest) in this area (see Chapter 2). Insecurity prevented coverage of three of the ten reserves originally selected to be surveyed: the Nimini Hills (151 km^2), Tingi Hills (106 km^2) and Tama-Tonkoli forest reserves (600 km^2 ; Fig.6.1).

6.4.2. Relative abundance of nesting sites

A total of 60 nesting sites with 218 nests were found in six of the seven surveyed forest reserves (Table 6.2; Appendix 6.2). These are the first records of *gymnocephalus* in the Kambui Hills and Dodo Hills (See Collar and Stuart 1985 for review; Allport *et al*, 1989; Collar *et al*, 1994). No colonies were found in the Kasewe forest reserve and in Gola West - a discrete section of the Gola forest (see Fig 2.6, Chapter Two).

Of the 60 nesting sites discovered, 19 (31.7%) had been abandoned but most sites (61.7%) were obviously in current use at the time of the study. The activity status of four nesting sites (6.7%) could not be ascertained. The majority (59.6%) of nests found at all nesting sites (218) were broken and incomplete (Table 6.3, Appendix 6.2).

The ratios of active to abandoned nesting sites and complete to broken nests found in each forest provided some indication of the relative status of each population and the intensity of attendant pressures on them. The ratio of active to abandoned

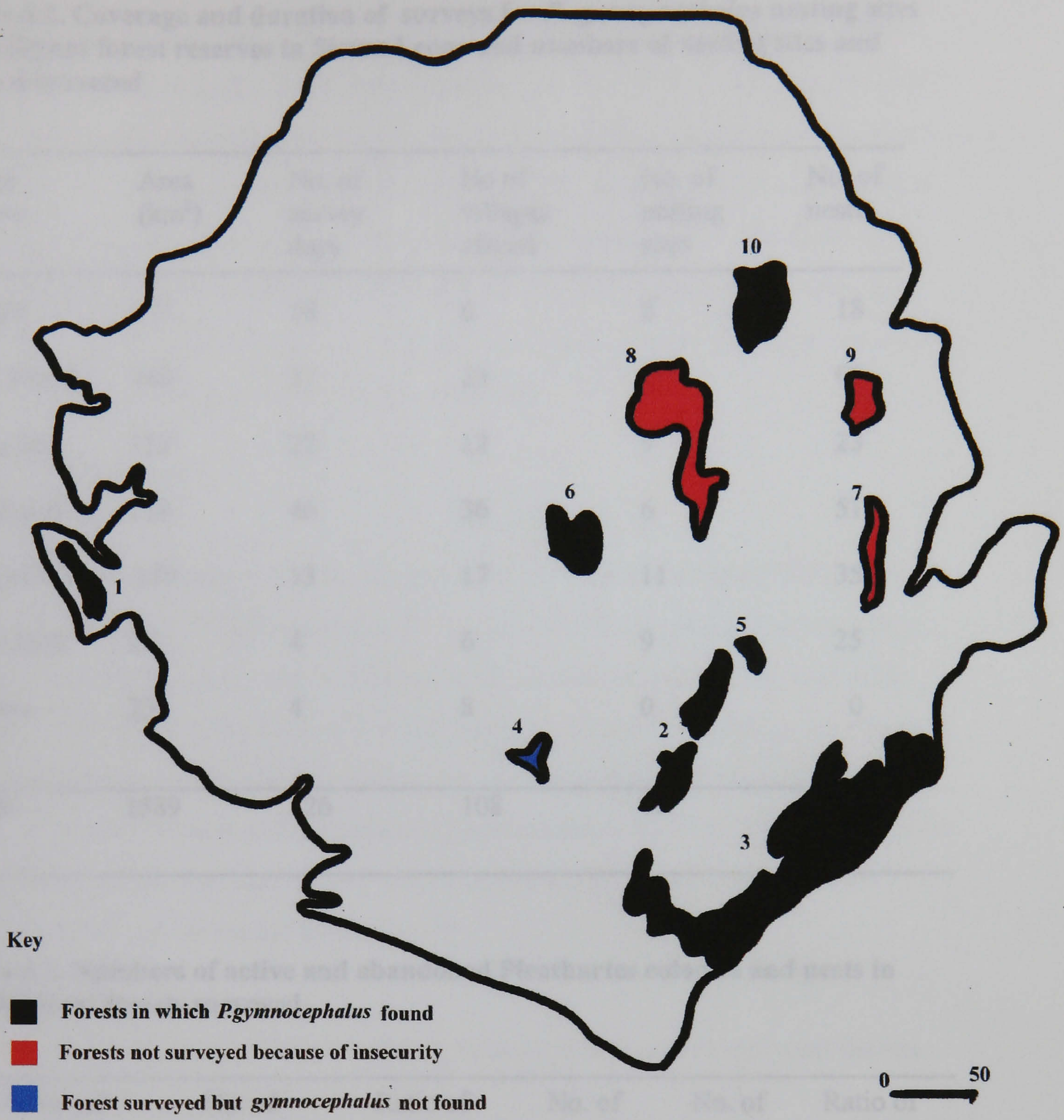


Fig 6.1. Forests selected to be surveyed for *Picathartes gymnocephalus* nesting sites in Sierrra Leone:1- WAPF; 2 - Kambui Hills; 3 - Gola Forest; 4 - Kasewe Forest Reserve; 5 - Dodo Hills; 6 - Kangari Hills; 7 - Nimini Hills; 8 - Tama Tonkoli Forest Reserve; 9 - Tingi Hills; 10 - Loma Mountains

Table 6.2. Coverage and duration of surveys for *P. gymnocephalus* nesting sites in different forest reserves in Sierra Leone and numbers of nesting sites and nests discovered

Forest reserve	Area (km^2)	No. of survey days	No of villages visited	No. of nesting sites	No. of nests
WAPF	177	16	6	8	18
Gola Forest	748	21	23	17	66
Loma Mts	332	22	12	9	23
Kambui Hills	158	46	36	6	51
Kangari Hills	129	13	17	11	35
Dodo Hills	22	4	6	9	25
Kasewe	23	4	8	0	0
Totals	1589	126	108	60	218

Table 6.3. Numbers of active and abandoned Picathartes colonies and nests in the different forests surveyed

	No. of active - colonies	No. of abandoned colonies	Ratio of active to abandoned colonies	No. of complete nests	No. of broken nests	Ratio of complete to broken nests
WAPF	2	2	1.0	6	13	0.36
Gola	15	2	7.5	36	30	1.2
Loma	5	4	1.25	7	16	0.44
Kambui	5	1	6.0	29	22	1.32
Kangari	6	5	1.2	8	27	0.3
Dodo	4	5	0.8	3	22	0.14
Kasewe	0	0	0	0	0	0
Totals	37	19	1.9	88	130	0.68

nesting sites was less than unity only in the Dodo Hills (0.8). The Gola forest (88%) and the Kambui Hills (85.7%) had the highest proportion of active nesting sites (Table 6.3). Active and abandoned nesting sites were found in almost equal numbers in each of the other forests (WAPF, Loma and Kangari Hills). Broken nests predominated at nesting sites in all forests except the Gola forest and Kambui Hills. The Dodo Hills had the lowest ratio of complete to broken nests (0.136) reinforcing the impression provided by the data on abandoned nesting sites, that the *gymnocephalus* population in the Dodo Hills is small and probably declining.

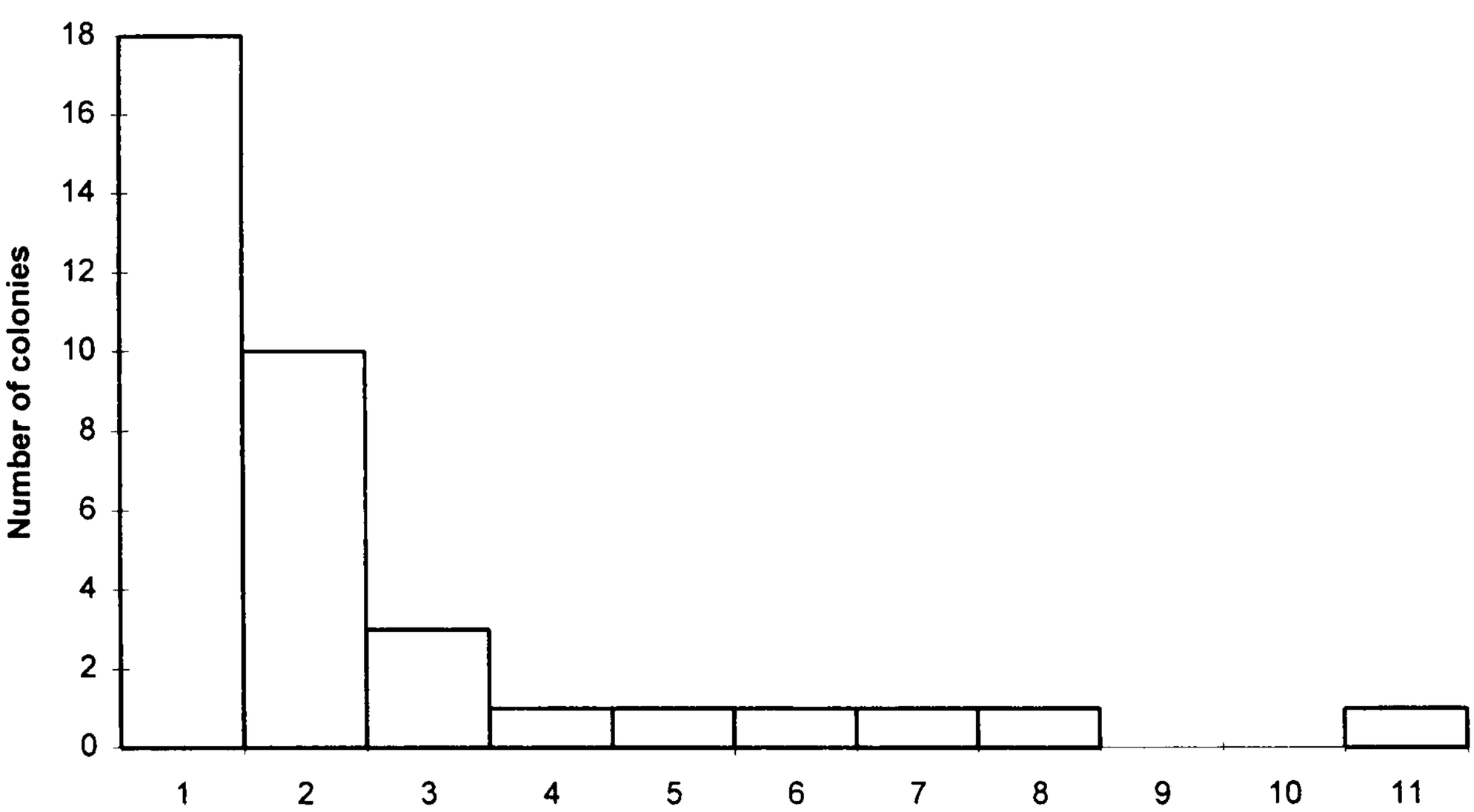
6.4.3. Colony size

Active nesting colonies ranged in size from one to 11 complete nests (Table 6.4). However, the majority of active sites (76%) consisted of only one or two nests (Fig 6.2). Mean active colony size was largest in the Kambui Hills (5.8) and least in the Dodo Hills (0.75) where three of four active nesting sites contained only one complete nest and and the fourth site did not have any complete nests. This latter site was deemed active because of the presence of *gymnocephalus* feathers. With the exception of nesting sites in the Kambui Hills and Gola forest, the number of nests at each breeding site did not exceed three (Fig 6.2).

Table 6.4. Mean size of active breeding colonies discovered in different forests

	Gola	Kambui	Loma	Kangari	Dodo	WAPF
Mean no.of nests/colony	2.40	5.8	1.25	1.33	0.75	2.0
S.E	0.619	2.368	0.625	0.543	0.25	0
n	15	6	4	6	5	6
Range	1 - 8	2 - 11	1 - 2	1 - 2	0 - 1	2 -2

Fig 6.2. Frequency distribution of numbers of complete nests at *Picathartes gymnocephalus* nesting sites



6.4.4. Colony Locations

The locations of nesting sites discovered during the extensive survey, as well as the villages visited at which there was no knowledge of *Picathartes gymnocephalus* are shown in Figs. 6.3a - f. Full details are given in Appendices 6.3 & 6.4. Boundary maps for the Dodo Hills Forest reserve were not available, and the settlements encountered on the way to nesting sites were not marked on standard maps so it was not possible to locate these sites with any degree of accuracy.

WAPF

In the WAPF, residents of six villages visited along the reserve boundary (Table 6.2, Fig 6.3a) and itinerant hunters had little knowledge of *gymnocephalus* (Thompson, 1993). Only two of 25 people questioned claimed to know the bird and no one knew of any nesting sites. I therefore decided to search for the species by walking along stream or river valleys looking for the characteristic mud nests on big rocks. This was done in collaboration with two ornithologists from the RSPB who were carrying out a general avifaunal survey of the WAPF (Ausden and Wood, 1991). Eight breeding sites were discovered in this way (Fig 6.3a), two of them by the RSPB ornithologists. All the breeding sites were in secondary forest within the forest reserve boundaries. Three of the eight sites (including one active site) were less than 50m from frequently used footpaths, and in one case, a major road (Thompson, 1993).

Gola Forest

In the Gola forest, colonies were discovered mainly to the west of Gola North (Fig 6.3b(i)). This is partly because most villages around Gola occur in this area, with few settlements along the eastern boundary with Liberia (Fig 2.6), so that coverage was biased to the west and north of the reserve. Also, an effort was made to avoid duplicating a previous survey by Allport *et al* (1989) during which several villages around the reserve had been canvassed for knowledge of *gymnocephalus*.

Nine of the 17 colonies found in the Gola forest region (during 21 days of surveys covering 23 villages; Table 6.2) were within the forest reserve boundaries while the remaining six sites occurred in forest patches around villages outside the reserve. These forest patches, are the communal property of the adjacent communities. They are legally exploited for farming, wood-cutting etc and are generally known as "community " forests.

The nesting site with the largest number of complete nests (8) occurred furthest from the forest reserve boundary (Fig 6.2b(i)) and was the only nesting site found in the Gola forest which was situated in primary forest, ie high forest with no detectable or recorded history of human activity. The two abandoned sites found during the Gola survey were both found outside the reserve boundaries; one occurred in farmbush whilst the other was in a small community forest patch. Three active nesting sites, each with a single *gymnocephalus* nest, were found close to each other in a plantation of cocoa (*Theobroma cacao*). This is the first record of *gymnocephalus* breeding in cultivated vegetation.

In Gola West, residents had no knowledge of the birds and knew of no nesting sites (Fig 6.3b(ii), Appendix 6.4). In Gola East, Allport *et al* (1989) had already visited the villages closest to the reserve and no new nesting colonies were found here.

Loma Mountains

A complete circumvention of the periphery of the reserve boundaries of the Loma mountains was carried out in 22 days of surveys in the area, during which 12 villages were visited (Table 6.2; Fig 6.3c). In addition, conventional bird census techniques (cold searching, transect walks, timed species counts and point counts) were carried out for 21 days within the reserve by two ornithologists from the University of East Anglia in collaboration with the *gymnocephalus* survey team. Fig 6.3 c shows the location of the base camp of the conventional survey. Searches were carried out mainly in a 2.5 km^2 area around this camp, with occasional extended transects up to

5km from the base camp into the interior of the reserve and two trips to Bintimani peak (1946m). The conventional surveys yielded one sighting of *gymnocephalus* at a point less than 2 km from the base camp. Intensive searching in this area did not reveal any nesting sites. The village surveys uncovered nine nesting sites of which three were no longer in use (abandoned sites). Six of the nine sites were in the fragmented community forests outside the forest reserve. Surprisingly, only one of the three abandoned sites were in these "community" forests, the other two were within the forest reserve, although one of the latter was very close to the reserve boundary (Fig 6.3c).

More nesting sites were found on the western side of the reserve than the east. This was probably partly because more villages were visited in the west (five) than the east (three) but there was also greater knowledge of the bird in the west than east. This was clearly shown by the fact that there was a local name for *P. gymnocephalus* in the west ("*Farmakangboi*" - meaning bird of the rock) whilst there was none in the East. Also there were more villages close to the reserve boundaries in the west than the east and , perhaps most importantly, approaches into the reserve from the east were much steeper than in the west and there was less forest cover round eastern villages.

Kangari Hills

In the Kangari Hills, 17 villages were visited in 13 days (Table 6.2). Eleven of these villages were within the formal boundaries of the reserve towards its northern end (Fig 6.3d). There was no knowledge of *gymnocephalus* in these villages. In contrast, 11 nesting sites were found in the course of visits to six villages outside the southern boundary of the reserve. Six of the eleven nesting sites were in farmbush habitat (Appendix 6.2) and, contrary to expectation (Collar and Stuart, 1985; Allport *et al*, 1989; Collar *et al*, 1994), three of these six sites were still being used for breeding. One of these three farmbush sites (Lomabu-A in the Kangari Hills; Appendix 6.2) was on one-year fallow land. *P. gymnocephalus* had abandoned the site two years prior to the survey when the area was cleared for farming (pers. comm. with local people) but the birds returned after a year's absence and were attempting to breed by the time this

survey was carried out (egg shells were found on the ground below the nests). The two other active farmbush sites had apparently last been cultivated 5-10 years before the survey and were approaching young secondary forest status at the time of this study. The birds were known locally in this area as *Ka-rondo* - "Great builder", but there was no name for them to the north of the reserve.

There are two possible explanations for this apparent dichotomy between north and south in the distribution of *gymnocephalus* in the Kangari Hills region :

1) there are actually few or no *gymnocephalus* nesting sites within the reserve

2) there are *gymnocephalus* sites within the reserve but people in settlements within the reserve know much less about the forest fauna than people outside the reserve in the south.

The correct explanation is probably a mixture of both factors. Although a quantitative vegetation survey was not carried out, the subjective impression gained was that large tracts within the reserve were covered with non-forest vegetation (farmbush and tall grass). The reasons for this are not clear but possibilities include mechanized prospecting, logging and agricultural encroachment, all of which have occurred in the reserve in the past despite its Non-hunting Forest Reserve Status (Davies and Palmer, 1991). This is supported by the fact that the villages within the Kangari Hills reserve are relatively new settlements of migrant miners who prospect for gold and diamond along the streams and rivers. They have little interest and less knowledge in the forest. This is in contrast to the situation in the south where villages are of long-standing and the traditional pursuits of hunting and farming which require intimate knowledge of the forest are practiced.

Kambui Hills

In the Kambui Hills forest reserve, 36 villages were visited in 46 days but only six nesting sites were found. The southern section of the reserve (Kambui South) was not as intensively surveyed as the northern end because of problems of access but equal numbers of nesting sites (three each) were found in each section (Fig 6.3e). Only one

nesting site was found outside the reserve boundaries (an abandoned site) probably because of the lack of community forest cover in this area. Much of the vegetation outside the reserves has been degraded by human activity from the high populations around the town centres of Kenema and Blama. There are also high levels of human activity (tree-felling and farming) within the reserves and, in this case, it was felt that the low number of nesting sites found probably reflected low bird densities on the ground.

Kasewe Hills

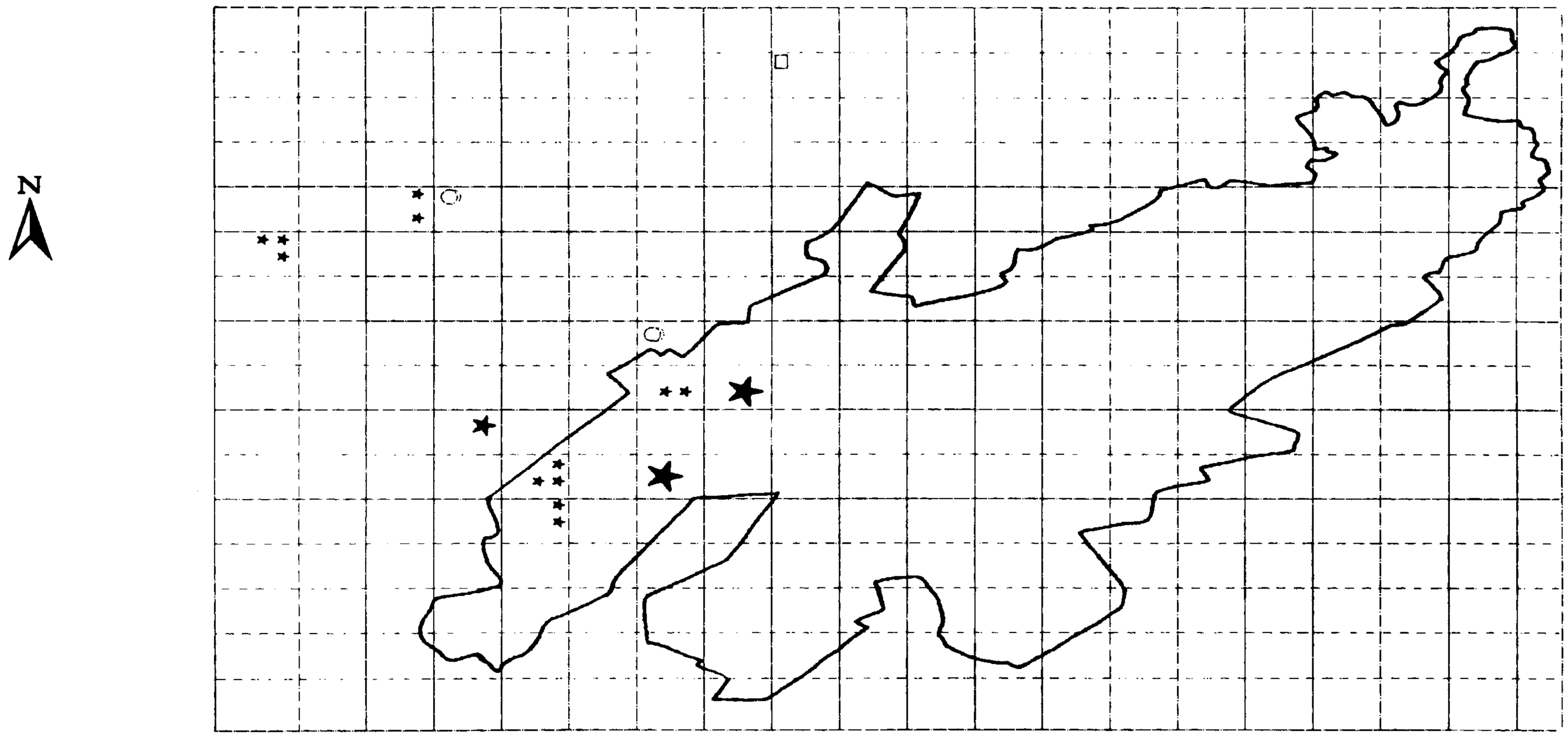
The survey team spent four days visiting eight villages distributed around the periphery of the Kasewe Forest Reserve (Fig. 6.2f). There was no knowledge of the birds among local villagers or the government forest guard who had spent over 10 years working in the reserve. Few signs of suitable habitat or nesting rocks were seen on walks through the reserve to get from one village to another. Apart from the Kasabere Hills (488 m) in the north of the reserve, much of the area is low-lying. It is almost certain that *gymnocephalus* is not present in the Kasewe Forest Reserve.

Dodo Hills

The Dodo Hills Forest Reserve was the smallest and most heavily encroached reserve visited. All six villages visited during a four-day survey were within the forest reserve and illegal farming within the reserve was widespread. Five of the nine nesting sites had clearly been abandoned (Table 6.3). Two of the abandoned sites were in cultivated land and two others were in farmbush. These sites had almost certainly been abandoned because the surrounding vegetation had been clear-felled for farming. It was reasonable to conclude from the high proportion of abandoned sites, that *gymnocephalus* was under severe pressure from human activity in this area.

Fig 6.3a. *Picathartes gymnocephalus* nesting sites discovered in the WAPF and villages visited at which no nesting sites known

Fig 6.3b(i): *Picathartes gymnocephalus* nesting sites discoverd around Gola North and villages visited at which no nesting sites known



Key:

★ = active nesting site (1-3nests)

★ = 4-6 active nests

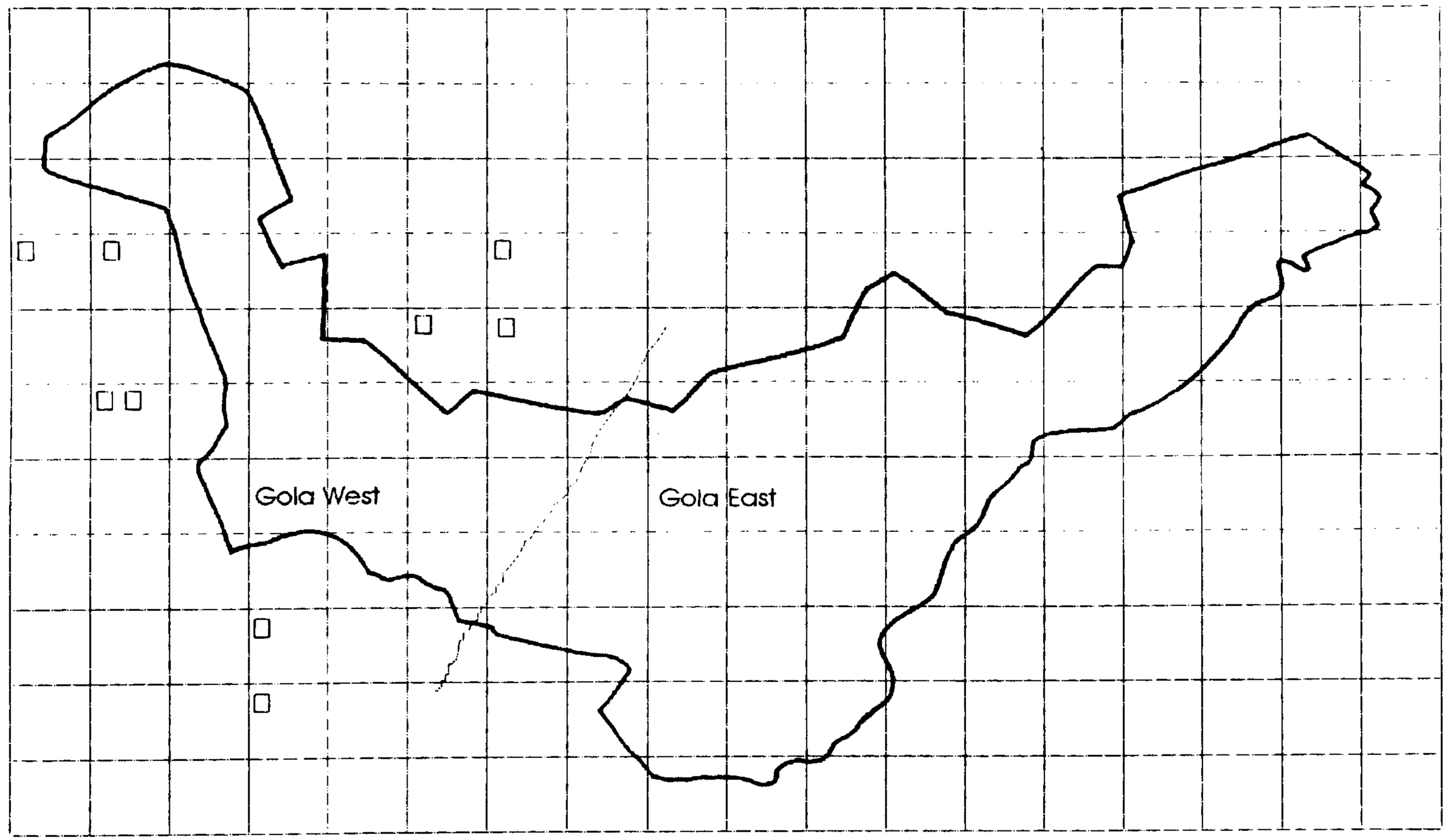
★ = >6 active nests

◌ = abandoned nesting site

□ = village visited at which no nesting sites known

0 _____ 2 km

Fig 6.3b(ii). Villages visited around Gola West during the extensive survey

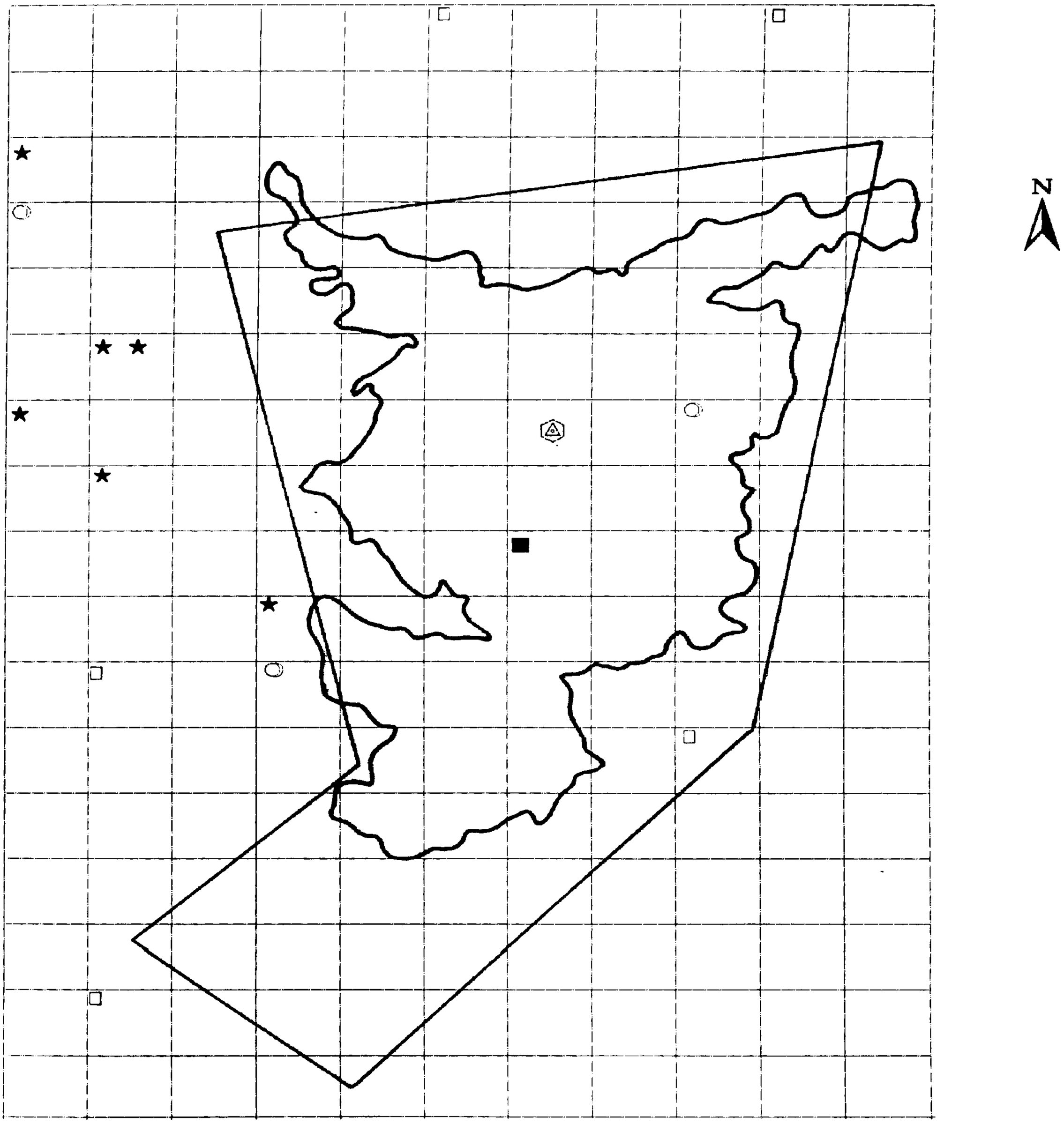


Key

□ = village visited at which no nesting sites known

= river between Gola West and Gola East

Fig 6.3c. *Picathartes gymnocephalus* nesting sites discovered around the Loma mountains and villages visited at which no nesting sites known



Key

★ = active nesting sites (1-3 nests)

○ = abandoned nesting site

□ =village visited at which no nesting sites known

■ = location of survey base camp

△ = Mount Bintimani peak

0 _____ 2km

Fig 6.3d. *Picathartes gymnocephalus* nesting sites discovered around the Kangari Hills Forest Reserve and villages visited at which no nesting sites known

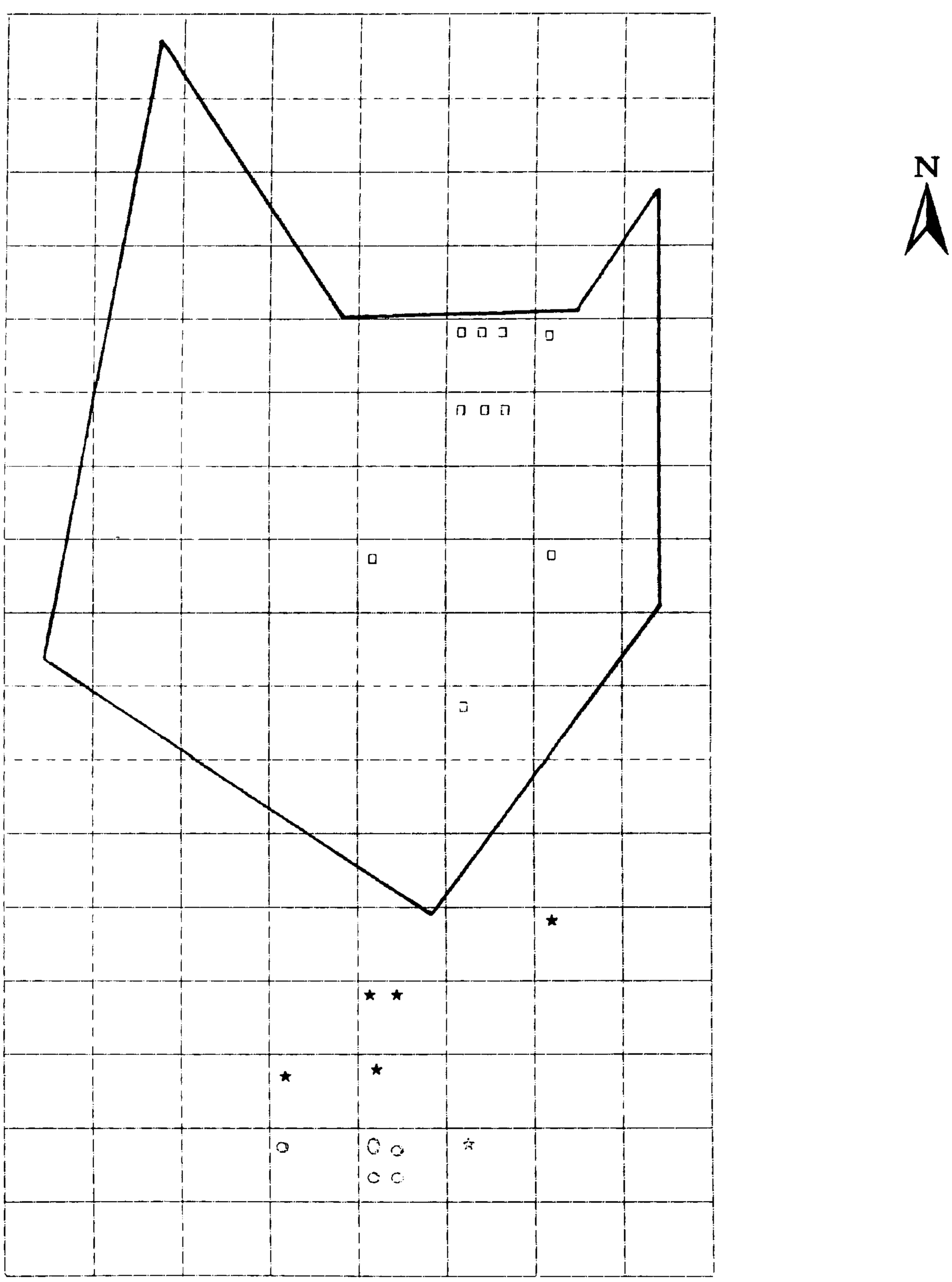


Fig 6.3e. *Picathartes gymnocephalus* nesting sites discovered in the Kambui Hills and villages visited at which no nesting sites known.

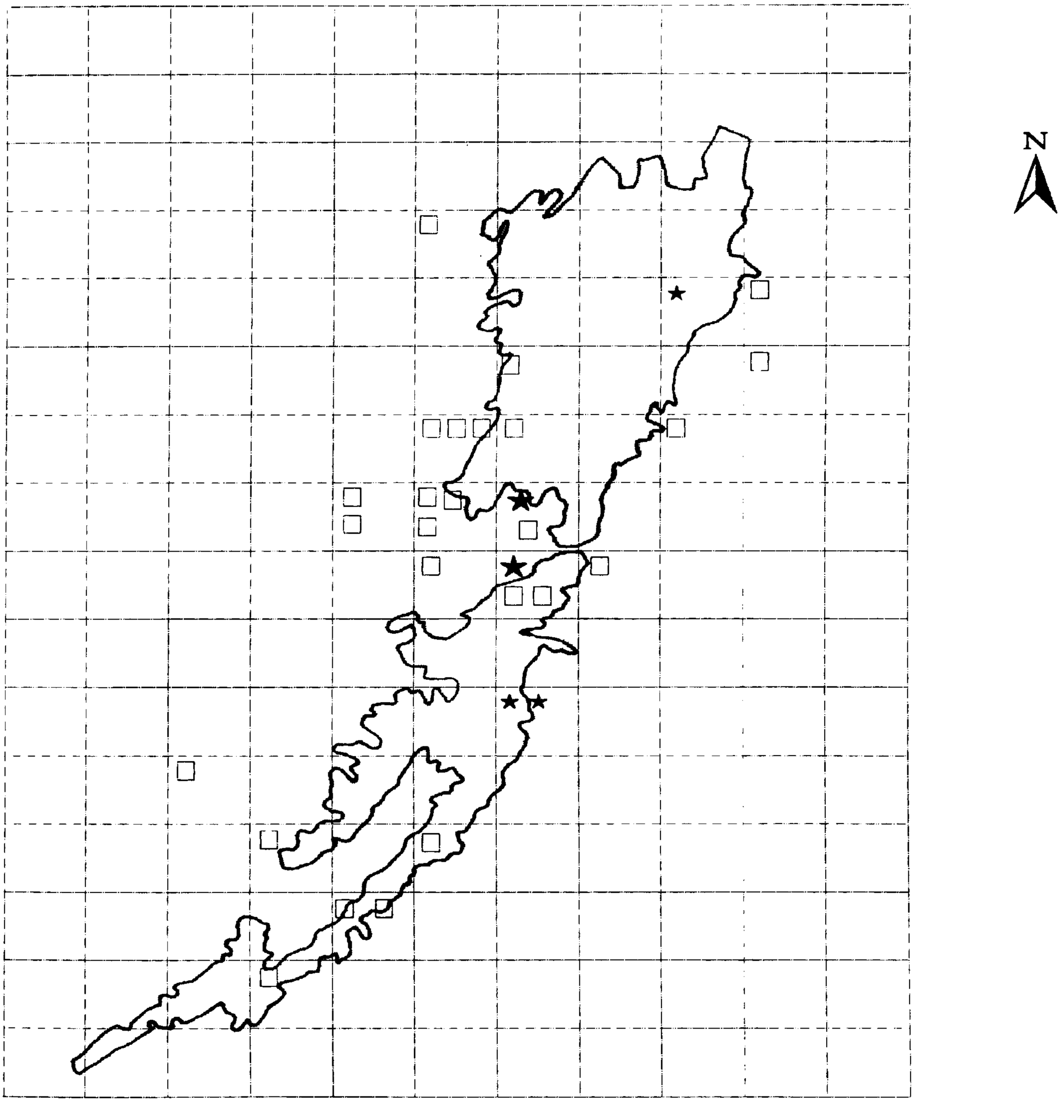
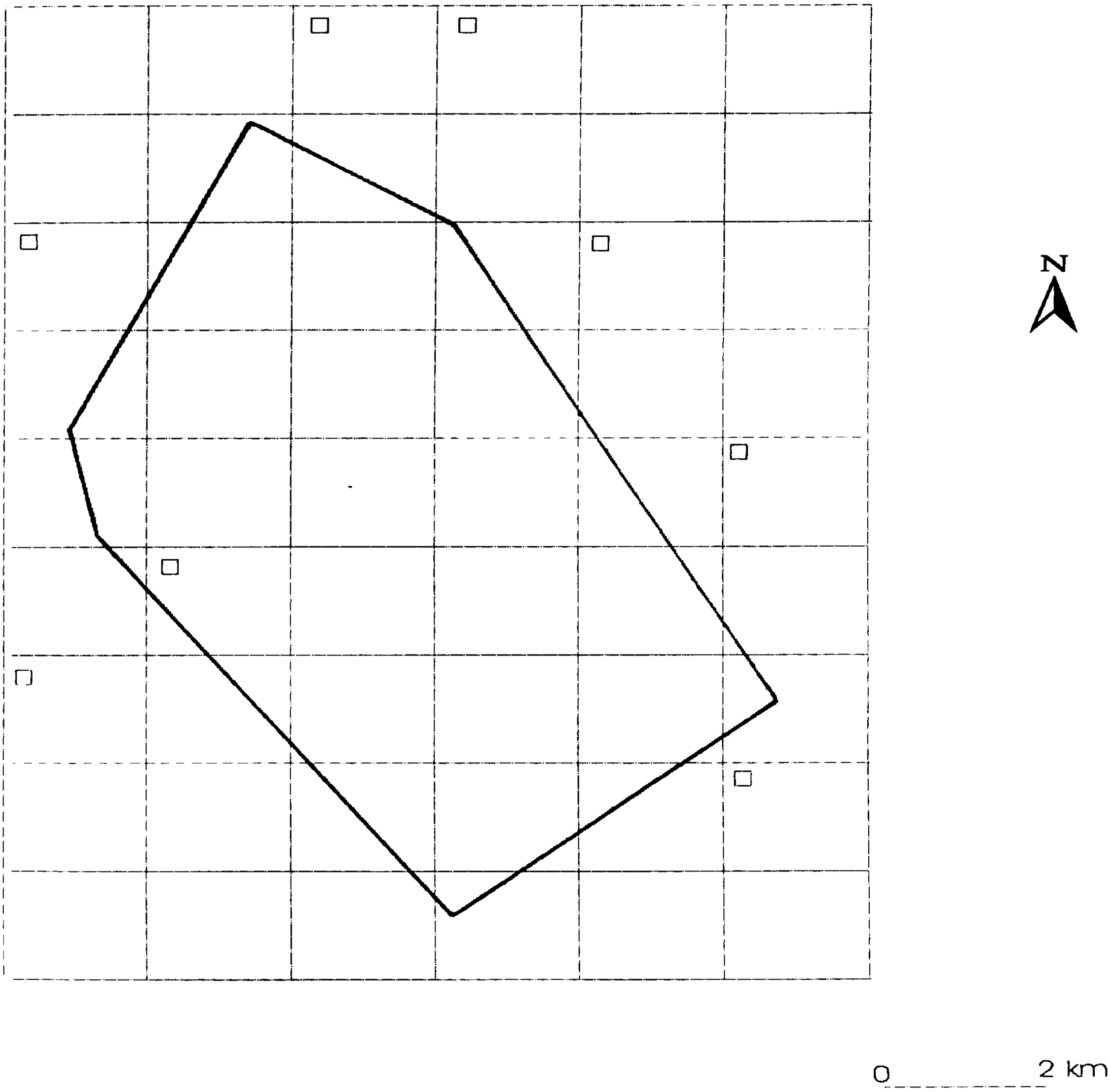


Fig 6.3f. Villages visited around Kasewe Forest Reserve during a survey for *Picathartes gymnocephalus* nesting sites



Key

□ = village visited at which no nesting sites known

6.4.5. Habitat

Vegetation

Most of the *gymnocephalus* colonies found during the survey were in secondary forest (70%). Another 20% were found in farmbush or forest regrowth whilst primary forest and cocoa plantations each held 5% of the total numbers found respectively (Table 6.5). These data indicate an interaction between the status of colonies (active or abandoned) and the type of surrounding vegetation (forested or non-forested) in which they were found. Colonies in non-forested vegetation (farmbush or cocoa plantation), were more likely to be abandoned than those in forest (Fishers 2-tailed exact test; $p < 0.05$, n =56). However, the discovery of active nesting sites in farmbush and plantation was unexpected (Section 6.4.4.) and this has implications for the perceived tolerance of g*ymnocephalus* to disturbance and the extent of the species' dependence on forested habitat for survival.

Topography

Forest

A quantitative assessment of habitat structure at active nesting sites in forested habitat is summarized in Table 6.6. *Picathartes* nesting sites mainly occurred on hill slopes in stream or river valleys inclined at angles of 20 - 49 degrees to the horizontal (mean: 30.3±4 degrees; range 0-65 degrees; Fig 6.4). Most nesting sites (67%) were less than 100m away from running water (Appendix 6.5). Colonies were predominantly in mature forest with substantial canopy cover (mean: 72.5±2%; range 56-87%). Average tree density was greater than 500 trees per ha and tree basal area averaged 78.5 m^3 per ha. Two sites (Tanima in the Gola area and Kpogbu - B in the Dodo Hills), were notable exceptions. At these sites, the birds bred in sparse woodland with the few trees present (<150 trees per ha) largely clustered round the nesting sites (Appendix 6.5).

Fig. 6.4. Frequency distribution of some ecological features of *Picathartes gymnocephalus* nesting sites

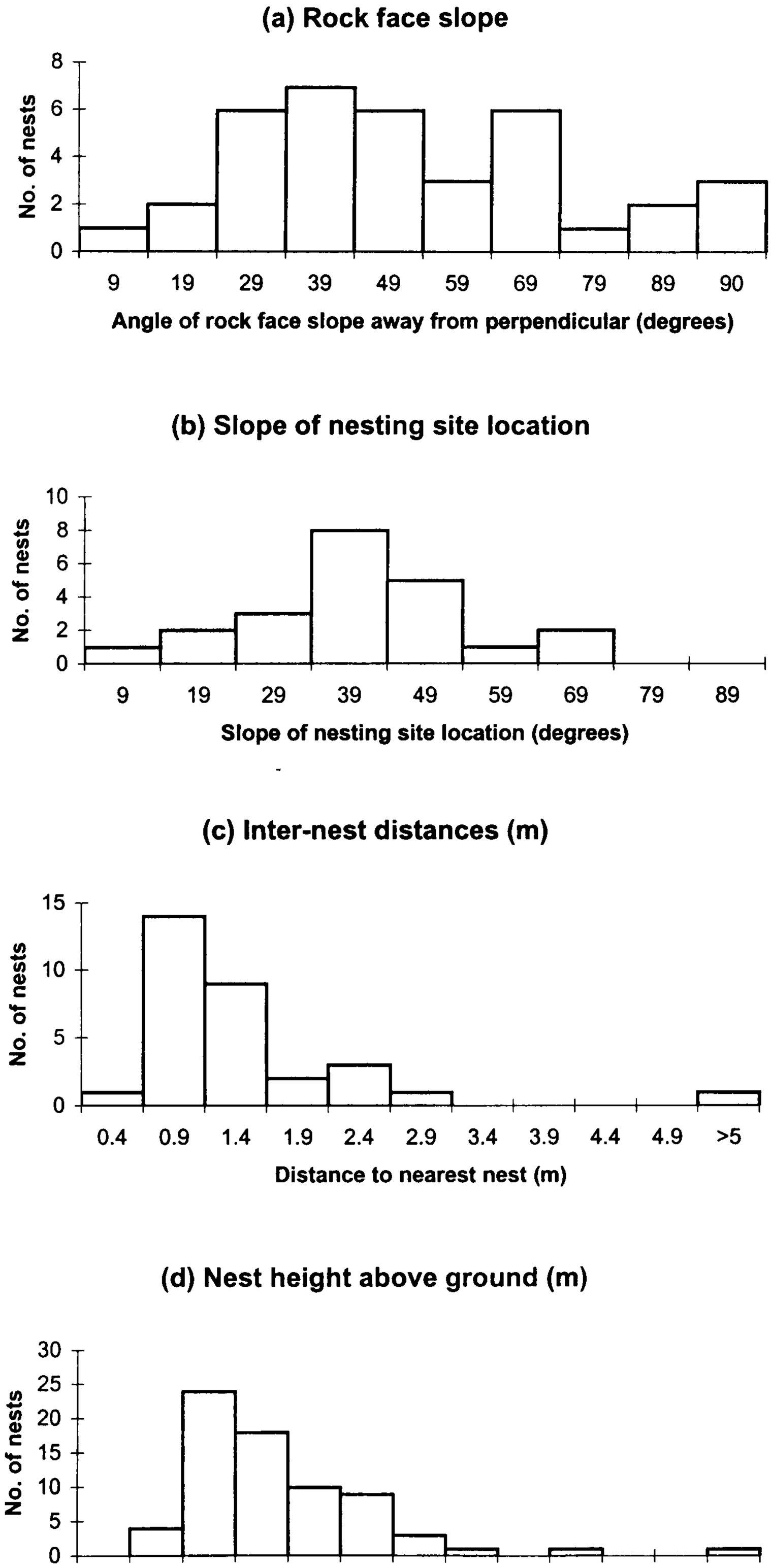


Table 6.5. Numbers of *Picathartes gymnocephalus* colonies found in different types of surrounding vegetation

	Primary forest	Secondary forest	Farm-bush	Plant-ation	Totals
Active	3 (5.36)	28 (50.0)	3 (5.36)	3 (5.36)	37
Abandoned	0 (0)	11 (19.64)	8 (14.29)	0 (0)	19
Totals	3 (5.36)	39 (69.64)	11 (19.64)	3 (5.36)	56[+]

* Figs in parentheses are percentages.
[+]Four nests of uncertain status in the WAPF were excluded from this analysis.

Table 6.6. Mean and standard error (n) for *Picathartes gymnocephalus* habitat characteristics at active nesting sites in Sierra Leone (n = no. of active nesting sites).

Habitat characteristics	WAPF	Gola	All Sites*
Tree density (nos/ha)	389.4 (59.3±7)	682.4 (114±10)	506.6±74.4 (20)
Basal area (m^2 per ha)	43.6±6.5 (7)	105.3±21.4(10)	78.5±13.2 (20)
Canopy cover(%)	74.3±3.0 (7)	74±2.6 (9)	72.5±2.0 (19)
Canopy height (m)	14.9±1.7 (7)	15.9±0.8 (9)	15.5±0.65 (18)
Angle of site slope (degrees)	29.1±5.6 (5)	34.7±5.3 (10)	30.3±3.97 (16)
Distance to nearest water-course (km)	0.13±0.07 (7)	0.3	0.227±0.0974

*Includes sites from reserves other than WAPF and Gola (see Appendix 6.5)

Farmbush

Quantitative characterization of farmbush habitat was difficult because most of the parameters used to measure habitat structure (see Bibby *et al,* 1992; Table 6.1) were not applicable and also because movement through the vegetation of tangled lianes and thickets was virtually impossible. However, a qualitative assessment at three sites showed that canopy cover was sparse (0, 5 and 20% respectively), maximum vegetation height was <4m and sapling or tree d.b.h was largely less than 5 cm. At the farmbush breeding site on one-year fallow land at Lomabu in the Kangari Hills (Section 6.4.4.), herbs (< 1m in height) surrounded the nesting rock. However, mature secondary forest occurred only 60 m away.

Nesting rocks

Nesting rocks varied widely in size (Table 6.7). The narrowest rock on which nests were found was 1.04m across whilst minimum height was 2.6m. Maximum dimensions were 23m breadth and 18m height (mean area ±se(n): 63.3±51.7 m^2.; range: 8.7-207.4 m^2). The smallest rock on which birds nested was 8.7m^2 in area. All nesting rocks were inclined at least 10 degrees from the perpendicular in the direction of the nesting surface with the majority at an angle of 20 - 50 degrees (53%; Fig 6.4). The minimum distance above the ground at which a nest was found was 1.04m but most nests (68%) were 1.5 - 2.5m above ground. The smallest distance recorded between active nests was 0.23m at the Lomabu farmbush site in the Kangari Hills but the modal class (78%) for inter-nest distances was 0.5 - 1m (Fig 6.4).

The mean number of active nests supported by a discrete rock face was 1.9 (Table 6.7). This differs from mean colony size (2.35±0.387; Table 6.4) because individual rocks often had more than one discrete face.

Rock area and slope did not have a significant influence on nest numbers. There was no significant correlation between nest numbers and rock dimensions (r_s = 0.213 for rock area and 0.03 for rock slope and $p > 0.2$ in both cases; Appendix 6.7).

Table 6.7. Mean, standard error and range for *Picathartes gymnocephalus* nesting rock characteristics at active nesting sites in Sierra Leone (n = nesting rocks or nests as appropriate).

Nesting rock features	WAPF	Gola	All sites*
Height(m)			
Mean (se±n)	7.95±3.9(7)	9.8±5.2(15)	7.8±0.8(34)
Range	2.8-13.5	3-18	2.6-18
Width(m)			
Mean(se±n)	6.9±5.3(7)	8.2±6.3(15)	9.0±5.99(34)
Range	1-16	2-23	1-23
Area(m^2)			
Mean (se±n)	50.1±39(7)	76.9±67.2(15)	63.3±51.7(34)
Range	8.7-118	13.5-207	8.7-207.4
Angle of rock slope (degrees)			
Mean (se±n)	31.4±16(6)	46.6±19.3(9)	42.9±18.1
Range	10-52.5	16-90	10-90
Nest height above ground (m)			
Mean (se±n)	2.9±0.25(10)	2.4(0.19(33)	2.32±10.4(79)
Range	1.25 - 3.8	1.48-6.5	1.04 - 6.5
Inter-nest distance(m)			
Mean(se±n)	0.5(2)	1.9±0.5(23)	1.5±0.27(34)
Range		0.54 - 10	0.5 - 10
Mean no.of nests per rock face			
Mean(se±n)	1.4±0.2(7)	2.13±0.5(7)	1.9±0.26(34)

*Includes sites from reserves other than WAPF and Gola.

Comparison of *Picathartes gymnocephalus* and *P. oreas* habitats

Habitat characteristics measured at six active breeding sites of *P. oreas* in three forests in the south and south-central regions of Cameroon (see Chapter 2) were generally similar to those of *gymnocephalus*; with sites located on forested slopes close to a stream or river (Table 6.8). The only statistically significant difference in the nesting habitat of the two species was in the amount of canopy cover. This was almost 20% less at *oreas* nesting sites (Mann-Whitney U test, df = 1, n = 27 , $p < 0.025$: Table 6.8). This was probably because three of the six *oreas* sites were in a small forest (Mesa forest; 200 ha) only 1km from Yaounde, the capital city of Cameroon (population : 1 million). This "forest" is now mainly a mosaic of cultivated plots, forest regrowth and degraded forest patches. Two of the three active *oreas* breeding sites in this forest (Mesa 1 and Mesa 3) were situated in a forest patch less than 30 m from a maize plot, a banana grove, a well-used footpath and a tree-felling site. Canopy cover at these sites was sparse and probably responsible for the low mean value obtained.

Table 6.8. Comparison of the habitat characteristics of active nesting sites of *Picathartes gymnocephalus* and *P. oreas* in Sierra Leone and Cameroon. Data given as mean and standard errors with n = no. of active nesting sites.

Habitat characteristics	*Gymnocephalus*	*Oreas*	Mann-Whitney U	p
Tree density (nos/ha)	506.6±74.3 (20)	308.2±76.6(6)	89 >	ns
Basal area (m^2 per ha)	78.5±13.2 (20)	59.6±17.3(6)	73	ns
Canopy cover(%)	72.5±2.0 (19)	55.0±4.3(6)	74.5	<0.025
Canopy height (m)	15.5±0.65 (18)	26.0±4.5(6)	22	ns
Angle of slope (degrees)	30.3±3.97 (16)	5.6±4.6(6)	27	ns
Distance to nearest water-course (km)	0.227±0.0974(16) 0.005 - 1.5	0.442±0.14(6) 0.005 - 1	6	ns

Comparison of active and abandoned *Picathartes* sites.

Of the 19 abandoned *gymnocephalus* breeding sites discovered during this study, eight occurred at locations that had been cleared for farming (Table 6.5). Human disturbance had clearly caused these sites to be abandoned. It was less clear why eleven other sites situated in forest were no longer used by the birds for breeding. The ideal way to address this question would have been to change conditions at one set of experimentally created breeding sites in a controlled manner whilst keeping conditions at another set constant; then observing how birds responded to these changes. This orthogonal approach was not possible here. Therefore, I attempted to address the question by comparing habitat variables at active sites and abandoned sites.

Abandoned sites were significantly closer to a water-course than active sites (Table 6.9; Mann-Whitney $U = 54.5$, $df = 1$; $n = 17$, $p < 0.01$). Differences between all other measured variables were not statistically significant but the results indicated that active sites occurred on bigger rocks in less degraded forest than abandoned sites. Active nesting sites had higher tree densities, more canopy cover and greater tree basal area (ie the trees were larger) than the locations of abandoned sites (Table 6.9). Also, abandoned nesting rocks were on average smaller than nesting rocks at active sites and their nesting surfaces were inclined at a smaller angle from the perpendicular than active sites. They were also closer to artificial clearings in the forest (a potential index of human disturbance) than active sites (Table 6.9).

Table 6.9. Means and standard errors of habitat variables and nesting rock features at active and abandoned breeding sites of *Picathartes gymnocephalus*.

Habitat & nest characteristics	Active Sites	Abandoned Sites	Mann-Whitney U	p
Habitat characteristics				
Tree density (nos/ha)	508±51.0 (12)	405±80(5)	39.5	ns
Basal area (m^2 per ha)	41.8±10.1 (12)	23.7±11.5(5)	43.5	ns
Canopy cover(%)	66.2±3.9 (12)	59.0±3.7(5)	44.0	ns
Canopy height (m)	20.5±2.77 (12)	29.1±0.13(2)	15	ns
Angle of slope (degrees)	21.2±4.39 (10)	4.4±0.85(2)	Ins. data	
Distance to nearest water-course (km)	0.256±0.086(12)	0.009±0.005(5)	54.5	<0.009
Distance to Clearing (km)	1.52±0.367 (12)	1.3±0.6 (5)	35.5	ns
Nesting rock features				
Height(m)	11.7±3.29 (12)	5.59±0.8 (5)	25	ns
Width(m)	25.6±11.4 (12)	8.4±2.6 (5)	20.5	ns
Rock slope (degrees)	27.9±4.5 (12)	20.5±11.96 (2)1	4	ns
Nest height above ground (m) .	2.78±0.092 (12)	0.15±0.023 (2)	14	ns

6.4.6. Populations

Bird numbers at a nesting rock in the Kambui Hills

This section of the study aimed to find out how many birds were using a single nesting site in the Kambui Hills. This information would be of use in relating bird numbers to numbers of nesting sites.

I trapped adult *Picathartes gymnocephalus* for 71.43 hours on 25 days between July 1992 and January 1994 at the Kambui Hills study colony (a single rock with 7 nests). Most of the trap effort (51.1 hrs; 72%) occurred on 14 days between February and May 1993.

Twenty captures of 14 different gymnocephalus were made (Table 6.10; see Appendix 3.1).

Table 6.10. Capture data for *Picathartes gymnocephalus* at a nesting site in the Kambui Hills.

Total numbers of captures (including recaptures)	= C = 20			
Total number of captures of unmarked animals	= U = 14			
No. of times a particular bird was caught	= k =	1	2	3 or more
No. of birds caught exactly k times	= f_k =	14	6	0

When these data were tested for homogeneity of capture probability, the catch distribution was not significantly different from a zero-truncated Poisson distribution (G test: G = 0.2556, df = 1, $p > 0.5$). An assumption of equal trappability of every individual in the population (birds using the nesting rock) was therefore made (Greenwood, 1996). The Craig - du Feu method of estimating animal populations from continuous captures and recaptures was then applied in order to determine the

total number of birds which had visited the nesting rock over the trapping period (du Feu *et al*, 1983; Underhill and Fraser, 1989; Greenwood 1996). This method provides a maximum likelihood estimate of population size based on a census model in which animals are trapped, marked and released one at a time (Underhill and Fraser, 1989). It is known to be particularly useful when populations are small and also because fixed intervals of capture and recapture are not required (du Feu *et al*, 1983: Underhill and Fraser, 1989). However, a key assumption is that the population under consideration is closed, so that there is no mortality, natality, emigration or immigration during the sampling period (du Feu *et al*,1983, Underhill and Fraser 1989, Greenwood 1996).

An initial approximate estimate of numbers of birds visiting the nesting site (N_o) was given by:

$$N_o = C^2/[\Sigma(k^2 f_k) - C\,]$$

where C = total numbers of captures (including all recaptures);

k = number of times each bird caught;

f_k = number of birds exactly caught k times;

This estimate was refined to a best estimate (N) using the expression:

$$H_o = log\,(N_o - U) + (C - 1)logN_o - C\,log(N_o - 1)$$

where U = total number of captures of unmarked animals.

and H_o = an index of the accuracy of N_o in which $H_o = 0$ if N_o equals the true population size N;

Confidence limits (95%) of the best population estimate (N) are:

$$N_o \pm 2\,(\sqrt{N}\,/(e^{c/N} - C/N - 1)$$

From the capture data (Table 6.10), the best estimate of the numbers of birds which used the Kambui Hills nesting site over the whole trapping period was 25 with 95% confidence limits of 10 and 40

Population size on the WAPF

In order to estimate population density of *P. gymnocephalus* on the WAPF, a total of 568 hours over 35 days were spent cold-searching 15 randomly selected 2.5 x 2.5 km blocks (Section 6.3.1). A total of 15 nesting sites holding 25 nests were found during the census (Table 6.11). Six of the sites (40%) were considered inactive. The nine active sites supported 12 active nests (Table 6.11).

Counts of active nests were used as the primary response data from which estimates of bird numbers were later derived. This enabled survey results to be related to *gymnocephalus* numbers,

The index of dispersion ie variance-mean ratio of active nest counts was 1.6. This suggested aggregation or a clumped distribution. However, small sample sizes did not permit valid tests for goodness of fit to a negative binomial error distribution or a poisson distribution. A logarithmic transformation (log x + 1) was therefore applied and 95% confidence intervals of the mean of the transformed counts obtained after back-transformation. Applying these confidence limits to the untransformed mean of the number of nests discovered per sq. km (an approximation after Fowler and Cohen, 1990; Sokal and Rohlf, 1995) enabled estimation of confidence limits for the whole reserve by simple proportion.

The mean number of active nests per 2.5 x 2.5 km block found in the 15 randomly selected blocks was 0.8 (ie 0.128 per sq km) in an area of 93.8 km^2. The 95% confidence limits on this density of nests were 0.04 and 0.346 per sq. km. From these estimates of nest density and confidence limits in the surveyed area, the number of active nests in the unsurveyed area (a total of 8 blocks occupying an area of 50 km^2) was estimated as 6 (0.128 x 50) with confidence limits of 2 and 17. This suggests an estimate of 18 nests (6 +12) in the whole WAPF reserve with 95% confidence limits of 14 (2+12) and 29 (17+12). If it is assumed that one active nest represents at least one breeding pair of gymnocephalus, the data implies a breeding population density of 0.203 per km^2 (0.00203 per ha) or one breeding pair per 9.85 sq. km.

Table 6.11. Census results of *Picathartes gymnocephalus* in 15 randomly selected 6.25 km^2 blocks in the WAPF reserve.

Block ref no.	No. of active sites	No. of inactive sites	No. of active nests	No. of inactive nests
1	0	0	0	0
2	2	1	2	4
2b	0	0	0	0
3	1	1	1	1
4	0	0	0	0
5	2	0	3	0
8	0	1	0	1
10	0	0	0	0
14	0	1	0	1
15	1	0	1	4
15b	0	0	0	0
16	0	1	0	1
18a	1	1	2	1
18	2	0	3	0
20	0	0	0	0
Totals	9	6	12	13

6.4.7. Relation of *Picathartes gymnocephalus* distribution to environmental variables

I fitted generalized linear models (Nicholls, 1989) to the WAPF survey data in order to relate the observed distribution of *P. gymnocephalus* on the WAPF to the local topography of the area.

I used the GLIM 4 statistical package (Francis *et al*, 1993) for the analyses. Three topographical variables were selected for inclusion in the analysis: the number of contours that crossed the boundaries of each 2.5 km^2 block (as a measure of steepness); mean altitude of each block and total river length in each block (Appendix 6.8). These variables could be easily read off from 1:50,000 maps of the area and

preliminary inspection revealed a wider range of values in these variables than other potential explanatory variables eg forest cover.

The response data were counts of total numbers of nesting sites (active and abandoned) found in each 6.25 km^2 block because these were most likely to be directly related to topography. A binomial error distribution with a logit link was then used to model the probability of presence or absence of *gymnocephalus* in 6.25 km^2 blocks on the WAPF in relation to the topography of the area. The scale parameter was taken as 1.0 as there is no test for overdispersion with binary response data (Crawley, 1993). The binomial error distribution was thought to be appropriate because a large number of blocks (40%) contained no nesting sites and those which contained sites showed little variation (range: 1 - 3, Table 6.11).

Model simplification was carried out by a backward deletion process (Crawley, 1993). Variables were kept in the current model if the change in deviance when they were removed was significant. Removing a component from a model causes a significant increase in deviance when the scaled deviance is greater than the value of X^2 with t_2 - t_1 d.f. where t_2 = degrees of freedom for current model and t_1 = degrees of freedom for new model (Crawley, 1993).

Exploratory generalized linear modelling analyses on the main effects only (steepness, altitude and river length) showed that none of these factors by themselves had significant influences on the presence or absence of *gymnocephalus* in a block (Table 6.12). However, when interactions between variables were inspected, main effects and two-way interactions between them explained virtually all of the variation in *gymnocephalus* distribution on the WAPF (Table 6.12). Removal of any one of the three possible two-way interactions between the three main factors (altitude x river length; altitude x steepness and steepness x river length) from the model caused a significant change in deviance. These results suggest that interactions between topographical features may be more important than any individual factors in determining the distribution of *P. gymnocephalus*. However, it should be noted that the model is overparameterized. Only six of the blocks were occupied, although the model has seven parameters. This makes the model unreliable.

Table 6.12. Goodness of fit statistics for binomial error distribution models of *Picathartes gymnocephalus* distribution on the WAPF.

Model	Scaled Deviance	Change in deviance	d.f.	P
Main effects only				
Null model	20.19	-	14	
"				
Full" model				
Alt + cont + river	15.596	- 4.594	11	ns
Main and interaction effects				
Null model	20.19	-	14	
"Full" model				
Main effects and two-way interactions	0.002452	-20.19	8	

Table 6.13. Parameter estimates and their standard errors (s.e) for models of the relation between *Picathartes gymnocephalus* distribution and topographical variables (Table 6.12)

Parameter	Parameter estimate	s.e	Parameter estimate/s.e
Main effects only			
"Full" model			
Constant	4.813	4.826	0.997
Altitude	-0.009016	0.01069	0.844
Contours	0.3042	0.4516	0.6736
River length	-0.877	0.5520	1.5877

6.5.DISCUSSION

6.5.1.Distribution

Picathartes gymnocephalus was found in six of the seven forests surveyed for the species. Records of the species in the Kambui Hills and the Dodo Hills were the first records for those areas (Section 6.4.2). These new records probably reflect the paucity of ornithological records in those areas rather than any real in-country extension of the species range.

Three of the ten forest reserves initially scheduled to be surveyed for *gymnocephalus* could not be reached because of security reasons (Section 6.4.1). One of these unsurveyed reserves,Tama-Tonkoli, is the second largest forest reserve in Sierra Leone (Section 6.4.1: 600 km^2). It is located in the northeast of the country (Fig 6.1) and is directly accessible only on foot. Over 30 years ago (1966), it was reported that a colony of 300 *gymnocephalus* nests (the largest ever known colony of *Picathartes gymnocephalus* or *P. oreas*) existed in a cave in this forest (J. Woolls *in litt* to L Grimes, 1966). A survey trip to Tama-Tonkoli during this study would have attempted to locate this colony. If such a colony still exists, it should obviously be a prime target for conservation action, and carrying out a search for it should be a high research priority in Sierra Leone as soon as security conditions allow. Woolls (1966, *in litt* to H.Tye) reported intense pressure from illegal farming by the local population in the north and east of the reserve 30 years ago, and also pointed out that a large section of the reserve was secondary forest which was systematically felled, farmed and re-afforested with commercially important plantation trees. Given that Sierra Leone's population has doubled in the intervening 30 years, these factors would suggest that the *gymnocephalus* population in the area would only have a slim chance of still existing in the numbers claimed in the 1960s. However, this must be balanced against the fact that in this study, *gymnocephalus* was found in all areas in which it had been previously reported, even up to 80 years ago ie WAPF (Kelsall, 1914; Bannerman 1932); Mongheri near the Kangari Hills (Glanville, 1954; Attenborough,

1955; J.S. Sawyerr 1965); Tunkia in the Gola forest region (Glanville 1954), and the Loma mountains (J.S. Sawyerr 1965; G.D. Field pers comm to Collar and Stuart 1985). If *gymnocephalus* has not yet disappeared from any of the areas in its former range which were surveyed here, it is likely that it still occurs in insurveyed areas from which it has been previously reported such as the Tama-Tonkoli forest reserve and the Tingi Hills. There are no previous ornithological records for the Nimini Hills, the third targetted but unsurveyed forest reserve.

During the extensive survey, *P. gymnocephalus* was not found in the Kasewe forest reserve or in Gola West, a section of the Gola forest complex separated from Gola North and Gola East by the Mahoi river (Fig 2.6). Failure to find the species may have been due to poor local knowledge of the forest rather than a real absence of the species in these areas. But, several factors suggest otherwise. The villages surrounding the two areas are occupied by people of the Mende tribe, well known in Sierra Leone for their very strong traditional way of life linked with the forest (Kandeh and Richards, 1996). In other areas (eg Gola North) where *gymnocephalus* occurs in forest surrounding Mende villages, the species is widely known to the people by the Mende name of *Plokunde* (bird of the rock) and the Mendes are the only tribe known to have had customary traditions involving the nesting sites of the species (See Allport et al, 1989; Kandeh and Richards 1996). This makes it unlikely that the Mendes around Kasewe and Gola West (less than 20 km from Gola North where the species is well known) would have been ignorant of its presence. Moreover, Allport *et al* (1989) also failed to find *gymnocephalus* in Gola West. It is therefore likely that *gymnocephalus* is actually absent from these areas.

Prior to this study, there were no systematic data available on the occurrence of *P. gymnocephalus* in any of the surveyed forests, except for the Gola forest. Allport *et al* (1989) found 30 *gymnocephalus* colonies in Gola, of which 21 were still active and supported 116 "new" nests (assumed to be the equivalent of the "complete" nests in this study). Combining the results of this study and that of Allport *et al* (1989), the Gola forest is now known to hold 47 *gymnocephalus* nesting sites, of which 36 are

active, and support a minimum of 204 nests. This is the largest concentration of *gymnocephalus* in Sierra Leone.

In addition to holding the largest known numbers of *gymnocephalus* nesting sites, the Gola forest also had the highest ratios of active to abandoned colonies (7.5) (Table 6.3). This suggests that the Gola forest *gymnocephalus* population is probably under less pressure than those in other forest reserves. At the other end of the scale, the lowest proportions of active nesting sites and complete nests were found in the Dodo Hills (Table 6.3). Of all the forests surveyed, the *gymnocephalus* population here is probably in the greatest danger of local extirpation.

6.5.2. Population density estimates

A total of 37 active nesting sites which supported 88 complete nests, were found in this study after a survey across 1589 km^2 of forest reserve. Assuming that one nest represents at least one breeding pair, this indicates the presence of at least 176 mature adults over an area of 1589 km^2 or a population density of 0.11 per sq.km. Applying this same methodology to an analysis of the data obtained by Ash (1991) for *oreas* in Nigeria in which 91 breeding sites were found in an area of about 900 km^2 gives a breeding population density of 0.20 km^2. This is almost twice that obtained for *P. gymnocephalus* in this study. However, Ash (1991) did not distinguish between complete and broken nests in his data. If a similar procedure is adopted with the data from the current study, then the 37 active sites with 167 complete and broken nests would have indicated a minimum of 334 breeding birds ie a breeding population density of 0.21 km^2 . This is virtually the same as the *oreas* density suggested by Ash's (1991) data in Nigeria. These analyses suggest comparable population levels of the two species in Sierra Leone and Nigeria.

In the formal randomized census of the *P. gymnocephalus* population on the WAPF, the density of the breeding population (when only active nests were taken into account), was estimated as 0.203 km^2 (Section 6.4.6). This is about twice the estimate

of the *gymnocephalus* breeding population density obtained by the village survey method across all the forest reserves surveyed (0.11km^2) and five times the estimate which would have been produced for the WAPF using the village survey method alone (Table 6.3: 0.056 per km^2 from 5 nests indicating 10 birds in an area of 177km^2). The formal census method almost certainly produced a more accurate estimate of *gymnocephalus* population density than the village survey method, since it is not constrained by the biases of local people's knowledge of nesting sites and the accessibility of potential sites. This suggests that the village survey method underestimates the *gymnocephalus* breeding density population by at least 50%. Also, surveys of local people failed to produce any records of nesting sites when settlements were new (eg Kangari Hills; Secton 6.4.4.) or if the inhabitants had an urbanized lifestyle (e.g. WAPF; Section 6.4.4).

In the Kambui Hills, a nesting site with seven nests was estimated as being visited regularly by 25 birds (Section 6.4.6). No other nesting site was found within 4 km^2 of the study site (Fig 6.4e) despite intensive searching over a period of two years. This may mean that there were 1.8 times more birds in the area than the 14 breeding adults which the seven complete nests at the site would have indicated from a simple nest count. Also, 12 birds were ringed at this site in the early part of 1993, of which only two bred at the site during the 1993 breeding season, although eight others were seen at the site at different times prior to and during the 1993 breeding season (Chapter Three). Moreover, a pair of breeding birds in the WAPF fought with two intruders for several minutes till the nest broke, destroying the contents (Chapter Three). These facts suggest the existence of a substantial non-breeding fraction in *gymnocephalus* populations and also indicate that nesting sites may be limited. This is supported by the fact that no vacant rocks of the size and shape suitable to bear *P. gymnocephalus* nests were seen in the 23 blocks which were searched during the random census. If it is assumed that a similar situation as in the Kambui Hills exists in other forests in Sierra Leone in which *gymnocephalus* occurs, then the total *gymnocephalus* population may be 1.8 times higher than estimates of breeding population density derived from counts of complete nests. This would mean that *gymnocephalus* population density in the WAPF would be 0.365 km^2 (0.203 x 1.8). Applying this

figure to the total forest reserve area in Sierra Leone (2960 km^2) produces a total population estimate of 1080 birds.

The accuracy of this estimate for the *Picathartes gymnocephalus* in Sierra Leone (1362) depends on several factors:

a) the efficiency of the randomized census on the WAPF. Because of the thorough knowledge of the WAPF terrain possessed by the census team and the time and effort spent on the census, I feel it is unlikely that more than 10% of the nesting sites in the area surveyed would have been overlooked. However, this census is easily repeatable, and the density figure obtained in this study could be adjusted in the light of future findings on the efficiency of detecting nesting sites with the effort we applied. Future censuses would also serve as a valuable means of monitoring the WAPF *gymnocephalus* population.

b) the accuracy and general applicability of the relation derived between counts of nests and the total numbers of birds in an area. This may vary between areas and require adjustment depending on local circumstances. It would also be possible to test it again in the future by using the 37 adults and nestlings which were marked in the Kambui Hills in the course of this study.

c) how representative the WAPF population (on which the density figures are based) is of other *gymnocephalus* populations in the area. Present evidence suggests that the Gola forest and not the WAPF has the highest population density of *gymnocephalus* in Sierra Leone (see above). Also, this survey has shown that *P. gymnocephalus* occurs both outside and inside forest reserves, so the present population estimate for the country based on WAPF densities and the area of forest within reserves is obviously a conservative one.

There are no previous estimates of *P. gymnocephalus* population density in Sierra Leone. However, to put the data in perspective, I compared the *gymnocephalus* estimate I obtained for the WAPF (most of which is secondary forest) with estimates of the population density in secondary forest, of other threatened bird species in Sierra Leone. (Table 6.14.).

Only one threatened species for which data were available - the Yellow-throated Olive Greenbul - was estimated to occur at similarly low densities to *gymnocephalus* (there were no data for the Rufous Fishing-owl *Scotopelia ussheri* and the Gola Malimbe *Malimbus ballmani* both of which are in the IUCN Endangered category). Although these density estimates were said to be fairly tentative (Allport *et al*, 1989), they suggest *gymnocephalus* occurs at lower densities than most other threatened species which have been studied in the field in Sierra Leone. The species should therefore be considered a high priority for any conservation action in the country.

Table 6.14. Population density estimates in secondary forest for threatened bird species in Sierra Leone. Data for all species other than *P. gymnocephalus* from Allport *et al* (1989).

Species	Scientific name	Conservation status (from Collar *et al*, 1992)	Population density (birds.km^{-2})
White-necked Picathartes	*Picathartes gymnocephalus*	Vulnerable	0.365
White-breasted Guineafowl	*Agelastes meleagridis*	Vulnerable	1 - 2
Yellow-throated Olive greenbul	*Criniger olivaceus*	Vulnerable	0.3 - 0.87
Nimba Flycatcher	*Melaenornis annamarulae*	Vulnerable	0.5 - 2.0
Rufous-winged Illadopsis	*Trichastoma rufescens*	Near-threatened	2 - 6

A population density estimate of the order of 0.4 per sq. km for *gymnocephalus* in Sierra Leone, as this study suggests, means that the largest and most pristine forest reserve in the country (Gola forest, 774 km^2) holds a population of less than 400 birds. Below a critical minimum size, populations may risk imminent extinction from inbreeding depression and long term loss of genetic variation (Soule, 1986; Stewart and Hutchings 1996). However, it is becoming clear that species which are naturally rare or have small population sizes are relatively immune to inbreeding depression, at least until only a very few remain. A comparison of early reports of *P.gymnocephalus* in Sierra Leone with the results of this study (Section 6.5.1) would suggest that the species has been existing in small demes for a long time (almost a century). Elsewhere, Butynksi *et al* (1996) have suggested that the population of *P.oreas* on Bioko consists of only one ot two dozen birds. *Picathartes* may well be relatively immune to inbreeding depression.

6.5.3. Nest distribution and habitat requirements

Almost 50% of the *P. gymnocephalus* nesting sites discovered during this study contained only one nest (Fig 6.2). This is in contrast to most previous observations, Thus, *gymnocephalus* has been recorded nesting colonially in Ghana (McArdle, 1958; Grimes, 1963, 1964; Grimes and Gardiner, 1963; Grimes and Darku, 1968), Ivory Coast (Brunel and Thiollay, 1969) and Sierra Leone (Glanville, 1954; Attenborough, 1955) whilst *oreas* has been observed breeding colonially, in Gabon (Brosset 1965a, 1965b) and Cameroon (Serle, 1952; Moore, 1974, pers obs). There are fewer records of solitary nesting by *Picathartes*. Colston and Curry-Lindahl (1986) found a solitary *Picathartes* nest at 1000m on Mount Nimba whilst Tye (1987) found six nests that were solitary and widely separated on gorges and cliffs between 600 and 1000m on Mount Cameroon, in an area with superabundant cliff faces for potential nesting. Tye (1987) therefore suggested that *Picathartes* may build nests colonially because of the limited availability of suitable rock faces rather than for any adaptive advantages gained from coloniality, such as information transfer and food finding benefits, and protection from predators (Wittenberger and Hunt, 1985; Krebs and Davies, 1991).

A number of factors may contribute to making a rock or cliff face suitable for nesting and determine the number of nest sites available on any given surface. Such factors are likely to include the area of a rock face (height and width), and the angle of slope of the rock from the perpendicular. Rock height would be an important factor influencing nest choice, because it would determine the potential distance from a nest to the ground or a point of purchase from which a terrestrial predator could attack a nest. In this study, most nests (>85%) were further from any potential purchase point than from the ground, so this factor was not considered further. Rock area would determine the number of nests which would fit on a single surface, depending on the minimum distance which the birds would tolerate between active nests. The angle of slope of the rock face from the perpendicular would be important in protecting nests from rain and water run-off.

The minimum distance above the ground at which a nest was found was 1.04m (n =79, Table 6.7), which agrees very closely with the 1.09m (n = 34) obtained by Allport *et al* (1989). Similarly, the mean internest distance of 1.5 (se, n = 0.27, 34) obtained in this study was very close to the 1.3m (se, n = 0.31, 12) recorded by Allport *et al* (1989). As Allport *et al* (1989) have already pointed out, these data mean that, particularly on a sloping surface, a large surface area of rock is unsuitable for nesting as it is simply too low. The conditions required for a potentially suitable nesting site are probably made more stringent by the need to keep eggs and chicks dry, since breeding takes place during the wet season. In this study, all nesting rocks sloped forward by at least 10 degrees from the perpendicular (Fig 6.4), and several of the nests on the more vertical surfaces (10 - 20 degrees angle of slope) had been built below an overhang or pelmet of rock which afforded protection from rain.

If these potential factors influencing nest site choice interacted in a simple way, it would be expected that bigger rocks would have more nests than smaller rocks, and rocks with a greater angle of slope from the perpendicular would provide more nesting sites than more vertical rocks. In this study, no significant correlation was found between rock dimensions and rock slope, and the numbers of nests found on

individual rocks, even though nests were found on a wide range of rock sizes and slopes (Section 6.4.5). This suggests a complex interaction between the physical factors that could potentially influence nest site choice and that it would be difficult to determine nest site suitability and availability from an assessment of the physical characteristics of the rock surfaces present in an area. However, evidence that there may be a substantial floater fraction in the *gymnocephalus* population, supports previous speculations that suitable nesting sites may be limited in some areas of the range of *Picathartes* (Tye, 1987, Allport *et al* 1989). This would lead to aggregation at suitable nesting sites as has been observed in some areas (eg Kambui Hills and Gola forest) and could also partially account for the nest robbing and destructive behaviour reported in Chapter Three.

In most previous observations, *Picathartes* has been recorded as inhabiting remote, and fairly undisturbed habitat (Webb, 1949; Serle 1952, Glanville 1954, Hall and Moreau, 1962; Grimes and Gardiner, 1963; Brosset, 1965; Grimes and Darku, 1968; Tye 1987, Fotso, 1993; Thompson 1993). Data from this study shows that nesting sites abandoned by *Picathartes* had lower tree densities, smaller trees and less canopy cover than sites which were still used for breeding (Table 6.9). This implies that habitat degradation probably has an effect on the bird numbers in an area by causing birds to move away from nesting sites. But data on the habitat features surrounding the nest sites of *Picathartes* unexpectedly showed the birds breeding at sites in forest regrowth which lacked a complete forest cover (Table 6.5) and also in areas quite close to human activity (eg less than 30 m from a maize plot in Cameroon and 50m from a charcoal production pit in the WAPF). This suggests that *Picathartes* is tolerant to fairly high levels of disturbance and can continue to exist in highly degraded habitat. Continued existence of *Picathartes* in these areas is probably evidence of increasing human pressure on the birds and perhaps recent behavioural adaptation by the birds to cope with this pressure. Birds may remain in highly disturbed habitats simply because they have nowhere else to go.

CHAPTER SEVEN

TAXONOMIC RELATIONSHIPS

7.1. AIMS

The main aim of the research in this chapter was to investigate, using DNA sequence analysis, the position of the genus *Picathartes* in the main taxonomic hierarchy of birds.

The specific question addressed was to determine to which (if any) of the two large divisions in the oscines (parvorders Corvida and Passerida) created by Sibley and co-workers, *Picathartes* belonged (Sibley *et al*, 1988; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990).

7.2. Previous Work

The earliest attempts to classify *Picathartes* placed the genus in the family Corvidae (Sharpe and Bates, 1908; Sharpe, 1877 and Sclater 1930 cited by Lowe 1938). Lowe (1938) carried out an anatomical examination of preserved *Picathartes* specimens, and on the basis of pterylosis (mainly the nature of the dorsal spinal feather tract), head colour pattern and feathering, and certain osteological characters (structure of the lachrymals, vomer and maxillo-palatines), concluded that the genus could not be referred to the Corvidae but should be placed as a sub-family Picathartinae in the Sturnidae. He suggested that *Picathartes* was a starling with "genetic affinities" to the Bald Starling (*Sarcops*), the Asian mynahs (*Mino*) and the Wattled Starling (*Creatophora*). *Sarcops* and *Mino* occur only on the Phillipine islands and in New Guinea (Sibley and Monroe, 1990) while *Creatophora* has a distribution which includes the Middle East (Yemen and Saudi Arabia) and East Africa (Sibley and Monroe, 1990). Lowe (1938) therefore postulated that *Picathartes* exemplified a

former Asiatic invasion of the African avifauna similar to what had apparently occurred in the case of broadbills (Euylaimidae) and peacocks (Phasianidae).

Bannerman (1948) followed Lowe (1938) and treated *Picathartes* as a sub-family of the Sturnidae. However, after seeing *Picathartes* alive for the first time (albeit in London Zoo), he gave *Picathartes* family rank - Picathartidae - and placed it next to the Corvidae from which Lowe had removed it.

Delacour and Amadon (1951) reviewed the behaviour, head feathering (or lack of it) and internal anatomy of *Picathartes* relative to other passerine families, and concluded that the genus had far more in common with babblers than with starlings, crows or other passerines. They noted a "striking resemblance" to the larger species of *Garrulax* (Timaliinae) but pointed out that *Picathartes* was an isolated genus in morphology and distribution and was probably something of a relict. They concluded by suggesting that *Picathartes* was an abberrant member of the thrush-babbler assemblage which should be included in the sub-family Timaliinae (within the family Muscicapidae) as a sixth separate tribe, the Picathartini.

Serle (1952a) reviewed the original anatomical evidence presented by Lowe (1938) in removing *Picathartes* from the Corvidae to the Sturnidae and presented information on the nests, eggs, roosting behaviour and plumage of *Picathartes*. He noted that *Picathartes* eggs were corvine and drew attention to a "remarkable similarity" in form and proportion between *Picathartes* and *Eupetes macrocercus*, the Malay Rail Babbler of South-east Asia. He concluded that *Picathartes* should remain in or near the Corvidae where it had originally been placed, until further comparisons had been made.

Simmons (1963), in a review of the taxonomic significance of babbler behaviour, pointed out that, unlike most babblers, *Picathartes* scratched its head by bringing the foot over the wing (indirect head scratching). However, Hall and Moreau (1972) considered *Picathartes* as timaliine on the available anatomical and behavioural

evidence and followed Delacour and Amadon (1951) in placing the genus as a sub-family of the Muscicapidae near the Timaliinae.

Sibley (1970) compared the egg-white proteins of *Picathartes gymnocephalus* with those of many other passerines using an electrophoretic method. The patterns produced by *Picathartes* egg-white were more like those of timaliids than those of corvids or sturnids. Also, *Picathartes* egg-white proteins were especially close to those of the African timaliine genus *Turdoides*. Sibley (1970) therefore concluded that this new evidence supported Delacour and Amadon's (1951) conclusion that *Picathartes* was a babbler. He went on to state that the closest living relatives of *Picathartes* were probably members of the genus *Turdoides*. However, Mackworth-Praed and Grant (1973) followed Lowe (1938) and placed *Picathartes* with the starlings while Serle and Morel (1977) maintained *Picathartes* in the Corvidae.

Olson (1979) agreed with the placement of *Picathartes* in the Timaliidae but rejected Sibley's (1973) suggestion of a close relationship with *Turdoides*. On the basis of comparative habitat, behaviour and morphology, he suggested that Serle (1952a) was correct in proposing a close relationship between *Picathartes* and *Eupetes*. Echoing Lowe (1938), he noted that the discontinuous distribution of the two species in West Africa and Southeast Asia was in accord with zoogeographic patterns observed in several other taxa.

Sibley *et al* (1988) presented a new classification of the living birds of the world based on the results of DNA-DNA hybridization studies. The main difference with regard to the Passeriformes, between this classification and the traditional arrangements (eg Wetmore, 1960; Voous, 1977) was the division of the oscines (Passeres) into the parvorders Corvida and Passerida. The Corvida apparently evolved in Australia and New Guinea; the Passerida in Eurasia, Africa and North America (Sibley *et al*, 1988). In this initial classification, *Picathartes* was placed with the babblers in the tribe Timaliini within the family Sylviidae in the parvorder Passerida. However, the evidence used for placing *Picathartes* in this position was not given.

Using evidence of DNA comparisons presented in Sibley and Ahlquist (1990), Sibley and Monroe (1990) placed *Picathartes* in the "limbo of parvorder *Incertae sedis*", on the boundary between the Corvida and the Passerida. It was felt that it was impossible to determine whether *Picathartes* was a member of the Corvida or the Passerida, on the available DNA evidence. The authors, cautiously speculated however, that the rock-jumpers of South Africa - *Chaetops* - could be the closest relatives of *Picathartes* and that the lineage of the two genera may have branched from that of the other Corvida soon after the divergence between the Corvida and the Passerida. A consideration of anatomical evidence (specifically, the structure of the humerus) in addition to DNA comparisons, led the authors to beleive that on balance *Picathartes* was probably a member of the Corvida.

Despite the revised classification by Sibley *et al*, (1990), recent regional works have maintained *Picathartes* close to or with the babblers (Howard and Moore, 1991; del Hoyo *et al*, 1992; Dowsett and Forbes-Watson, 1993). The babblers themselves are either presented as a separate family (Howard and Moore, 1991; Dowsett and Forbes-Watson, 1993) or as part of a large assemblage given as the Muscicapidae (del Hoyo *et al*, 1992)

7.3. Materials and Methods

7.3.1. Sample collection

Blood samples were collected from 17 *Picathartes gymnocephalus* (13 nestlings; 4 adults) and 5 *P. oreas* (all nestlings). *P.gymnocephalus* specimens were taken from birds trapped in the Kambui Hills and the Western Area Peninsula Forest Reserve (see Chapter Three). Samples were collected from nestlings when they were 2-3 weeks old and weighed between 100-150g. At this stage, nestlings were old enough to withstand handling without any apparent ill-effects but not old enough to give alarm calls or fledge prematurely (pers. obs.; see Section 3.4.2). Blood samples were taken from the brachial vein. The vein was wiped with 70% alcohol then pricked with a sterile,

unused disposable needle and slight negative pressure applied via an attached syringe (see Arctander and Fjeldsa, 1993). The ensuing small pool of blood was collected with a heparinized microcapillary tube or drawn up into the syringe. Slight positive pressure was then applied to the brachial vein with alcohol-soaked cotton wool till bleeding stopped. Capillary tubes were sealed with "cristaseal", labelled and initially kept in liquid nitrogen. This applied mainly to specimens collected in the Kambui Hills (7). All specimens were finally stored in APS buffer (10% EDTA, 1% NaF, 1% thymol) at room temperature.

P. oreas samples originated from the Dja forest in Cameroon. Samples were obtained from R.C. Fotso (see Section 2.3.2) during a field trip to Cameroon in January 1996. Fotso had supervised blood sample collection from nestlings using similar field protocols as described above, during the breeding season immediately prior to my visit to Cameroon.

7.3.2. Molecular analysis

DNA sequence variations in a portion of the mitochondrial cytochrome *b* gene were used as estimates of genetic variation to investigate the phylogenetic relationship between *Picathartes* and its putative relatives. Sequence data for *Picathartes* were obtained during this study by collaboration with R. Tiedemann (see Section 2.3.4) while data for other genera were obtained from sequence databases.

Cytochrome *b* is one of the 9-10 proteins that combine to form complex III of the mitochondrial oxidative phosphorylation system. It is essential for the proper transfer of electrons in the electron transfer chain and is a membrane-bound protein. The cytochrome b gene is one of the more conserved protein genes of mitochondrial DNA (Avise, 1994).

It was decided to use mitochondrial DNA (mtDNA) to investigate the taxonomic relationships of *Picathartes* for several reasons:

a) DNA-DNA hybridization methods had not resolved the taxonomic position of

Picathartes (Sibley and Ahlquist, 1990) but seemed to indicate a position at variance with the traditional position derived from morphology and behaviour. A different DNA method could provide an independent test of Sibley *et al's* (1990) findings.

b) mtDNA evolves about 10 times faster on average than single copy nuclear DNA and because it is a haploid, maternally inherited genome without recombination, it is also easier to characterize (Murray *et al*, 1994). It has therefore recently been widely used to examine avian relationships between and within genera, and within species (Edwards and Wilson, 1990; Edwards *et al*, 1991; Helm-Bychowski and Cracraft, 1993; Murray *et al*, 1994; los Monteros and Cracraft, 1997).

c) A small part, 307 base pairs of the cytochrome *b* gene of mtDNA is easily amplified from diverse species via the polymerase chain reaction - PCR (Kocher *et al*, 1989). This small part has proved valuable for phylogenetic analysis in birds, because it contains phylogenetic information extending from the infraspecific level to the intergeneric level (Kocher *et al*, 1989; Edwards *et al*, 1991).

d) The enzymatic amplification of a specific DNA segment using PCR is made possible by the highly specific binding of oligonucleotide primers to sequences flanking the segment. These primers allow the binding of a DNA polymerase that then copies the segment. Because each newly made copy can serve as a template for further duplication, the number of copies of the target segment grows exponentially. A standard set of primers directed toward conserved regions of mtDNA has been developed which is applicable to a wide variety of vertebrates (Kocher *et al*, 1989).

Amplification and sequencing of the mitochondrial cytochrome *b* gene

Isolation, amplification and sequencing of the mitochondrial cytochrome *b* gene was carried out by R. Tiedemann of the Institut fur Haustierkunde at Christian-Albrechts-University in Kiel, Germany. I visited the institute in early 1997 and observed initial attempts at sequencing *oreas* mtDNA. The following is a summary of my observations and protocol information supplied by R.Tiedemann.

Total DNA was extracted from *Picathartes* blood samples using the Super Quik Gene kit (Analytical Genetic Testing Center, Denver, USA).

About 367 base pairs of the mitochondrial cytochrome b gene were amplified via PCR using the standard primers Oligo1 (CCATCCAACATCTCAGCATGATGAAA) and H 15149 (CCCCTCAGAATGATATTTGTCC). Assay conditions were 1 µl Taq-polymerase (Appligene, Illkirch, France), 1.5 µl of each primer (10mM), 1.875 µl of nucleotide mix containing ATP, CTP, GTP, and TTP at 2mM concentration each, in a reaction volume of 62.5µl. An amount of 2µl of the *Picathartes* DNA preparation was added to the reaction mixture. After an initial denaturation step at 94°C for 5 min, 40 cycles were carried out with denaturation at 94°C for 1 min , annealing at 45°C for 1 min , and extension at 72°C for 1.5 min, followed by a final extension at 72°C for 1.5 min.

The PCR products were purified using a commercial kit (Qiagen, Hilden, Germany) and cycle-sequenced using the ABI Dye terminator kit (Applied Biosystems, Foster City, USA) and one of the primers. Reaction conditions were 30 cycles of denaturation at 96°C for 10 s, an annealing at 50°C for 5 s, and an extension at 60°C for 4 min. Samples were run on an ABI 373 automatic sequencing device. Both strands were sequenced and aligned to each other for confirmation.

7.3.3. Selection of genera for phylogenetic analysis

In order to choose species for inclusion in the phylogenetic analysis, I considered three sequences of avian families:

a) the modified Basel list of Voous (Campbell and Lack, 1985; Keith *et al*, 1992; Dowsett and Forbes-Watson 1993).

b) the Wetmore list (Morony *et al*, 1975; Howard and Moore, 1991; del Hoyo *et al*, 1992)

c) the classification of Sibley and Monroe (1990) based on the principles and results laid out in Sibley and Ahlquist (1990).

Genera in the five avian families immediately above and below the designated position of *Picathartes* in each sequence were regarded as the closest relatives of *Picathartes* in that sequence and as being suitable for inclusion in the phylogenetic

analysis (Fig 7.1). This turned out to include all the families to which *Picathartes* had been assigned by previous work (Section 7.2).

Fig 7.1. Families adjacent to *Picathartes* in the avian family sequences after three different authorities.

Howard & Moore 1991 (after Wetmore)	Dowsett & Forbes-Watson (1993) (after Voous)	Sibley & Munro (1990).
Prunellidae	Sylviidae	Pomatostomidae
Turdidae	Muscicapidae	Laniidae
Orthonychidae	Platysteiridae	Vireonidae
Timaliidae	Monarchidae	Corvidae
Panuridae	Timaliidae	Callaeatidae
Picathartes	***Picathartes***	***Picathartes***
Polioptilidae	Paridae	Bombycillidae
Sylviidae	Remizidae	Cinclidae
Muscicapidae	Certhiidae	Muscicapidae
Platysteiridae	Nectariniidae	Sturnidae
Maluridae	Zosteropidae	Sittidae

A total of 29 families containing 441 genera fitted the prescribed criteria (genera placed in different families by different authorities were considered only once).

I searched international genetic databases for mtDNA sequences of species of the 441 selected genera using the "Lookup" programme, available through the Medical Research Council's (MRC) Human Genome Mapping Project Resource Centre's (HGMP-RC) WorldWideWeb menu for registered users. Lookup identifies sequences by a variety of characteristics (eg name, accession no, author etc) and produces an output comprising a list of sequences. The sequence libraries searched were: a) SW release b) Pir c) EMBL and d) GenBank.

In cases where Lookup identified several species of the same genus with mtDNA sequences available in the databanks, only one species was selected for inclusion in the analysis. This kept the number of species involved at a manageable level as some of the programmes used in the analysis have upper limits on the number of species

they can handle simultaneously, and also because their speed slowed down as a function of the number of species involved.

Species within a genus were selected for analysis on the basis of a) the cytochrome *b* region which had been sequenced; a 95% overlap with the *Picathartes* sequence was deemed desirable, and b) geographical distribution; African and Asian species were given precedence on the assumption that they were more likely to be related to *Picathartes* (Appendix 7.1).

7.3.4. Phylogenetic analysis

Sequence alignment

A total of 30 species including *Picathartes* were chosen for phylogenetic analysis of their cytochrome *b* sequences. I then used the ECLUSTALW programme from the HGMP-RC menu for registered users to align the sequences. ECLUSTALW identifies all sequences with a specific common extension in a working directory and produces an output file comprising a multiple alignment of all the sequences in multiple sequence format (MSF) .

Tree building and analysis

Phylogenetic analyses were undertaken with the aid of the Phylogeny Inference computer package PHYLIP (version 3.5c; Felsenstein 1993) plus a pre-release of one of the programs (DNAML4) from PHYLIP version 4.0. All programmes were run in X windows on Unix interface from Edinburgh University by remote login to HGMP-RC.

The multiple alignment produced and stored in MSF format by ECLUSTALW was changed into an interleaved format (so it could be read by PHYLIP) by running a standalone program called READSEQ. Typing the command:

readseq -a myseq.msf -format=phylip -output=myseq.phy

reformatted the MSF file "myseq.msf" into a file called "myseq.phy". This was almost readable by PHYLIP. Final conversion into PHYLIP format was acheived by carrying out a global substitution of all periods by dashes.

Tree Construction methods

In order to construct phylogenetic trees from the cytochrome *b* sequences, I used two of the three main methods available in Phylip ie Maximum Likelihood and Distance-based methods. A third available method, Parsimony, was not used because it is known to perform very badly with difficult datasets with long and short branches (Wright, 1997).

Maximum Likelihood and Distance-based methods assume a basic model of molecular evolution where the rate of evolution at all sites in a sequence is assumed to be the same, and all sites are assumed independent. Assumptions specific to each model are stated where appropriate.

Maximum Likelihood

Maximum Likehood analysis was carried out using the DNAML4 program in the Phylip package. In estimating phylogenies from nucleotide sequences by maximum likelihood, DNAML4 employs a model which allows for unequal expected frequencies of the four nucleotides, unequal rates of transitions and transversions, and for different (prespecified) rates of change in different categories of sites. The optimality criterion is the log-likelihood; usually large negative numbers. The best tree is the one with the most positive log likelihood value (Felsenstein, 1993).

In this analysis, nucleotide frequencies were calculated empirically by DNAML4 and one category of substitution rates was assumed. The relative rate of transitions and transversions (the Ts/Tv ratio) was estimated using the Quartet Puzzling Program (PUZZLE) and also by repeated runs of DNAML4 with the U option (Wright, 1997).

This option forces DNAML4 to hold the tree topology constant for different runs of the programme with different selected values of Ts/Tv. The Ts/Tv estimate used (to nearest 0.1) is that corresponding to the highest log likelihood value.

The global rearrangement option was invoked in running DNAML4 and the input order of sequences randomized with 10 starts and a random seed number of 4n + 1 (where n = any number less than 30). This ensured that sequence input order did not influence tree topology.

Maximum Likelihood analysis was restricted in all sequences to that part of the cytochrome *b* sequence which had been sequenced for *Picathartes*. This was done by weighting all base pair positions of species sequences in a separate "weights" file. Weight information was coded as either zero or one at all base pair positions. Only base pair positions designated with a one were considered by DNAML4. This ensured that uniform sequence lengths were analysed for all species.

Distance Method

The program DNADIST in Phylip was used to estimate sequence divergence between species in the dataset. DNADIST creates distance matrices from sequence data, which can then be used in a Distance-based method of phylogenetic tree construction (Felsenstein, 1993). The genetic distance matrices are based on an estimation of the percentage difference in the number of non-identical positions between sequences derived from all possible pairwise comparisons. DNADIST can compute four different distances between species on the basis of four different models, by adjusting for multiple mutations at the same site and the tendency for some base changes to be more common than others, in different ways. The models are Jukes-Cantor, Kimura 2-parameter, Felsenstein's DNAML and Jin & Nei (Wright 1997).

In this analysis, Felsenstein's DNAML model was used in order to facilitate comparison with the maximum likelihood analysis. The model is an elaboration of Kimura's 2-parameter model which takes into account possible differences between

the rates of transitions and transversions and does not assume that the equilibrium frequencies of the four nucleotides are equal.

The distance matrix produced by using DNADIST was used to produce a phylogenetic tree with the Fitch-Margoliash method (FITCH) in PHYLIP. FITCH estimates phylogenies from distance matrix data under the "additive tree model", according to which the distances are expected to equal the sums of branch lengths between the species. FITCH does not assume rate constancy across lineages although it assumes equal rates in lineages (basic model of evolution). Methods (eg KITSCH) which assume rate constancy across lineages (ie evolutionary molecular clock) can give seriously misleading tree topologies if rate differences do exist in the dataset (Wright, 1997).

Treeplots

All trees were plotted from the output of the tree construction methods by using the programs DRAWTREE, DRAWGRAM and RETREE in the Phylip package.

7.4. Results

7.4.1. Characterization of mtDNA cytochrome *b* sequences of *Picathartes*

The nucleotide sequence of 325 base pairs (positions 100 - 424) of the cytochrome *b* gene of *P. oreas* (n = 4) as determined by R. Tiedemann is shown in Fig 7.2.

This is the first characterization of the DNA of *Picathartes* and the sequence will be deposited in international genetic databanks (Genbank and EMBL) on completion of this thesis.

DNA sequencing of *P. gymnocephalus* has so far failed at PCR, and only *P.oreas* is involved in the phylogenetic analysis in this section. Investigations to determine suitable assay conditions (the probable cause for PCR failure so far) for successful

sequencing of *gymnocephalus* are ongoing at the time of writing (R. Tiedemann, pers. comm.)

Fig 7.2. The DNA nucleotide sequence of 325 base pairs (positions 100-424) of the cytochrome *b* gene of *P.oreas* (n=4).

TTCGGATCCCTCCTAGGTATCTGCCTTATCTCACAAATTGTAACCGGCCTACTACTAGCCAT
ACACTACACAGCAGACACCTCCCTAGCCTTCTCCTCCGTCGCCCACATTTGCCGTGACGTA
CAATTCGGCTGACTAATCCGAAACCTCCATGCAAACGGAGCTTCCTTATTCTTCATCTGCA
TCTACATCCACATTGGCCGAGGCATCTACTACGGCTCATACCTAAACAAAGAAACCTGAAA
CATTGGAATCCTACTCCTCCTAACCCTGATAGCAACCGCCTTCGTAGGCTACGTCCTACCCT
GAGGACAAATATCA

Part of the ECLUSTALW alignment of the cytochrome *b* nucleotide sequences of the 30 taxa used in this analysis is shown in Appendix 7.2 (full details available from the author). When all 30 sequences were considered together, 59% of 350 base positions examined were variable with 142 base pairs being invariant. Variations at the first, second and third codon positions were similar (55%, 61% and 62% respectively). The relatively high levels of variation (see Kocher *et al*, 1989; Edwards *et al*, 1991; Helbig *et al*, 1996) are what would be expected in a dataset from species, where some may not be closely related.

7.4.2. Phylogenetic trees

Maximum Likelihood analysis

Maximum likelihood phylogenetic trees of *Picathartes* and 29 putative relatives are shown in Figs 7.3.& 7.4. In Figs 7.3 and 7.4a, the Loggerhead Shrike of North and Central America, *Lanius ludovicianus* was used as outgroup while the Golden-crowned Kinglet, *Regulus satrapa* served as outgroup in Fig 7.4b.

Relative empirical base frequencies in the dataset were determined as A - 0.27839; C - 0.30551; G - 0.15943 and T(U) - 0.25667. In Fig. 7.3, the transition-transversion ratio

was set at 1.32, the value obtained by running PUZZLE, while in Fig 7.4., it was set at 1.7, the value given by repeated runs of DNAML4 (see Section 7.3.4)

Log-likelihood of Figs 7.3.& 7.4 were -4104 and -4109 respectively. The trees are unrooted and therefore cannot be considered as providing information on lineage or ancestry. Attention is focussed on identifying clades or groups, the members of which are then considered as being more closely related than members of other similar clades.

The two initial clades in Fig 7.3 consist of : 1) a group comprising seven thrushes (Turdidae), a starling (*Sturnus cineraceus*) and a flycatcher (*Ficedula narcissina*) and 2) the remaining 21 species including *Picathartes*. Below this initial division, which the statistical output of DNAML4 indicates is not significant (Appendix 7.3), five clades (excluding the outgroup) can be discerned. The thrush-babbler assemblage splits into two groups while the remaining 21 species comprises three groups: a) a group made up of *Regulus satrapa* and *Phylloscopus sibilatrix* b) *Picathartes* by itself and c) a large clade comprising mainly genera recognized by Sibley and Munro (1990) as belonging to the Parvorder Corvida ie Orthonychidae, Laniidae, Paradiseidae and Vireonidae. However, this group also includes Paridae, Sylviidae and Zosteropidae which are members of the Passerida, the other main Parvorder recognized by Sibley and Munro (1990). In summary , of the five main clades in Fig 7.3, *Picathartes* is in a group by itself. It should also be noted that the long branch length for *Regulus satrapa* indicates minimal phylogenetic relationship with the other species in the analysis.

Tree topology in Fig 7.4 is similar to that of Fig 7.3. The main differences are: 1) *Orthonyx spaldingi* is placed in the same clade as *Picathartes* and 2) *Parus*, *Sylvia* and *Zosterops* now form a separate clade, albeit with *Laniarius*. The *Picathartes* clade now occurred between the thrush-babbler assemblage and the other species. When *Regulus satrapa* was used as an outgroup instead of *Lanius ludovicianus*, the latter occurred in the same clade as members of the Corvida and had the Chough (*Pyrrhocorax pyrrhocorax*) as its closest relative.

Fig 7.3. Maximum likelihood phylogenetic tree of *Picathartes* and putative relatives from 29 taxa. The Transition/Transversion ratio was set at 1.32 and *Lanius ludovicianus* used as outgroup

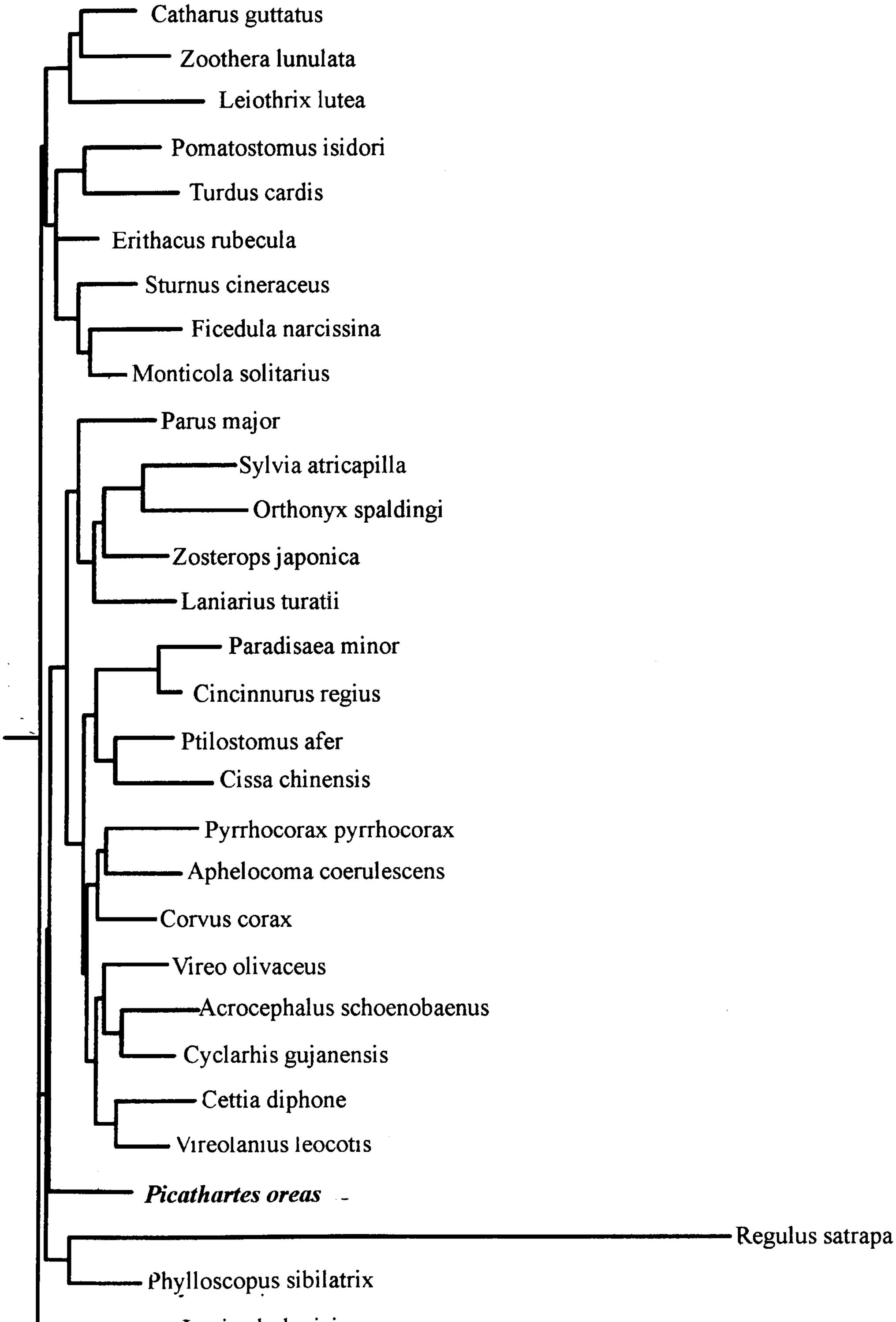


Fig 7.4a. Maximum Likelihood phylogenetic tree of *Picathartes* and putative relatives from 29 taxa. The Transition/Transversion ratio was set at 1.7 and *Lanius ludovicianus* used as outgroup.

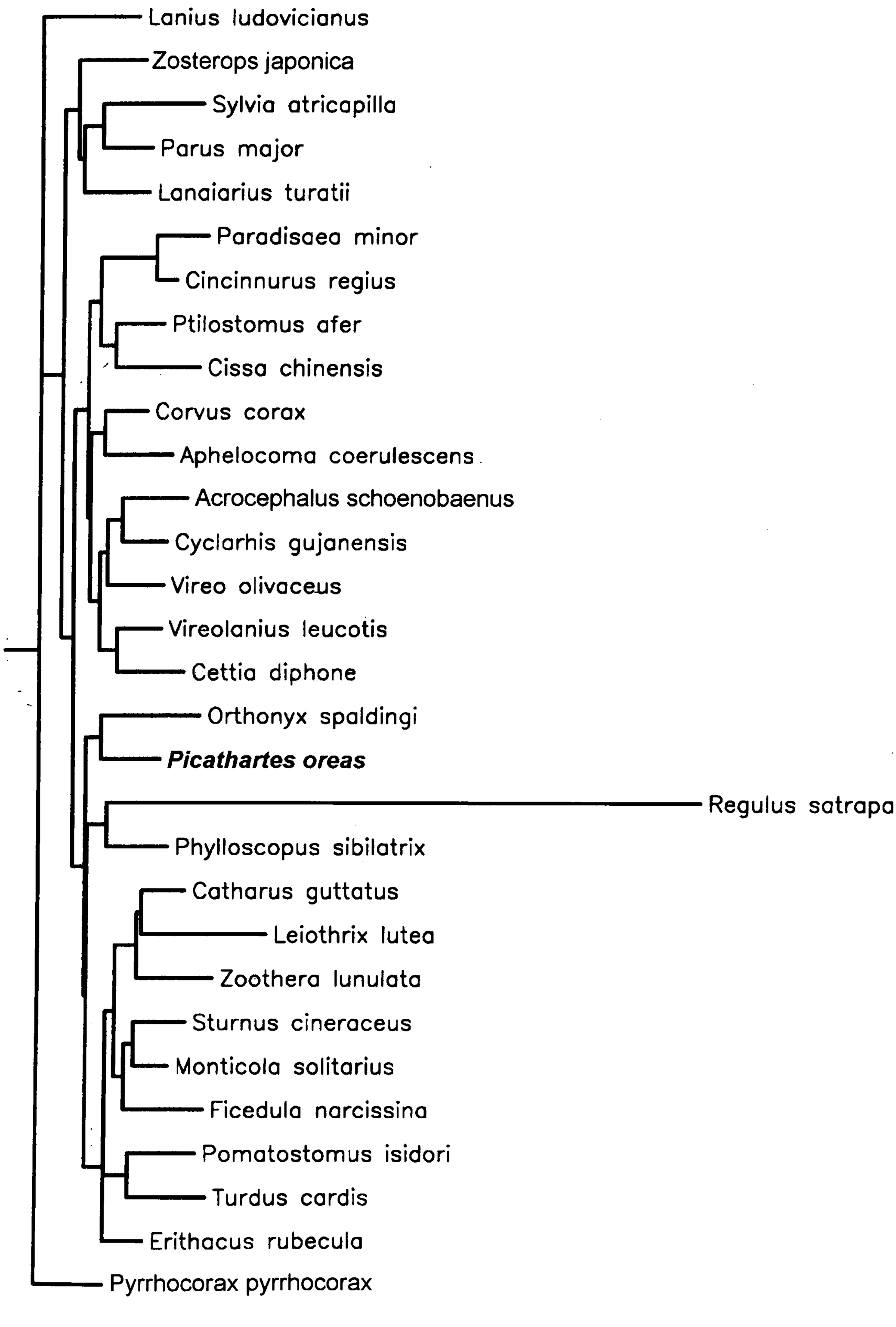


Fig. 7.4b. Maximum Likelihood phylogenetic tree of *Picathartes* and putative relatives from 29 taxa. The Transition/Transversion ratio was set at 1.7 and *Regulus satrapa* used as outgroup.

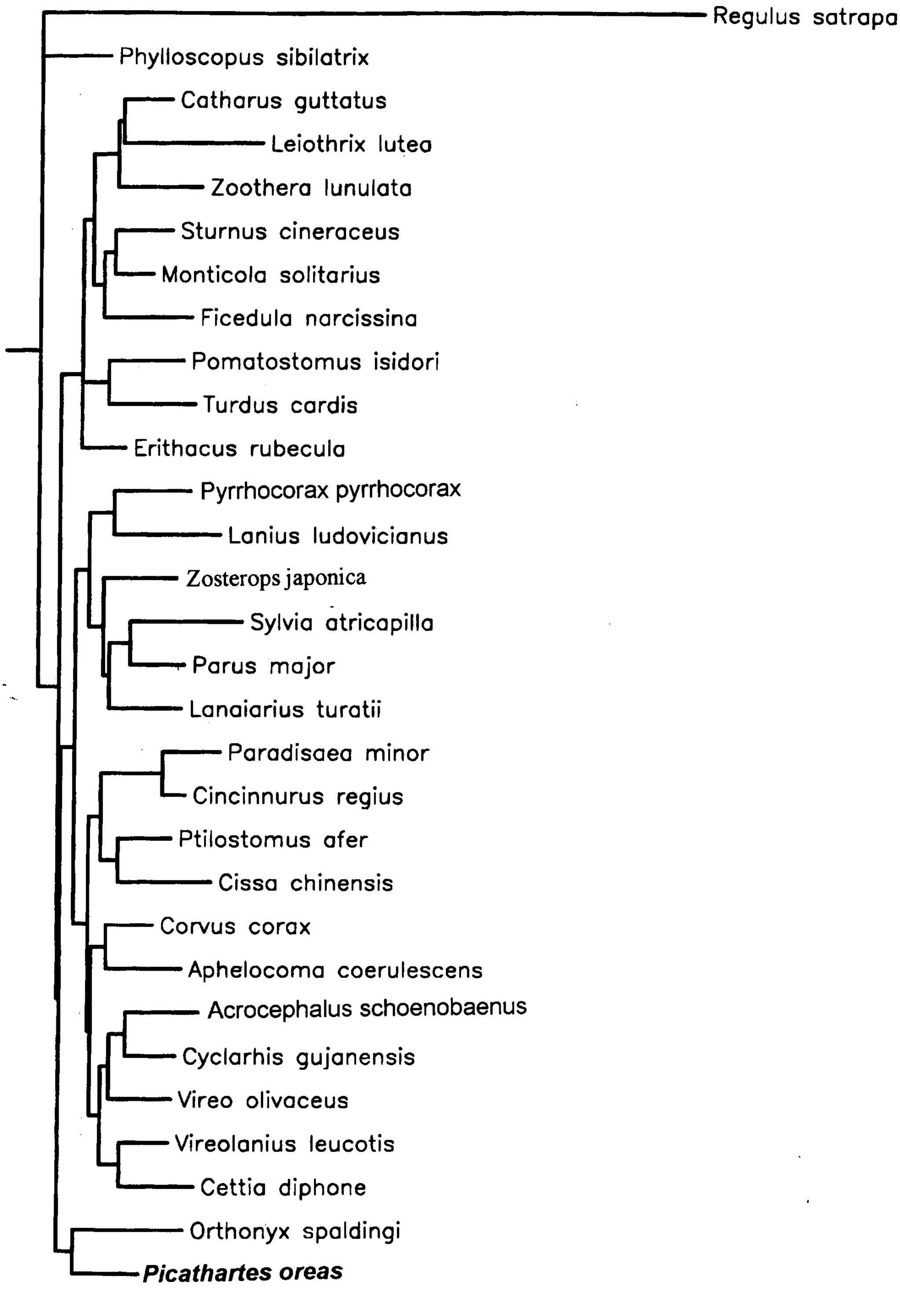


Fig.7.5a. Fitch-Margoliash phylogenetic tree of *Picathartes* and putative relatives from 29 taxa. Correction for multiple hits based on Felsenstein's DNAML model. *Lanius ludovicianus* used as outgroup.

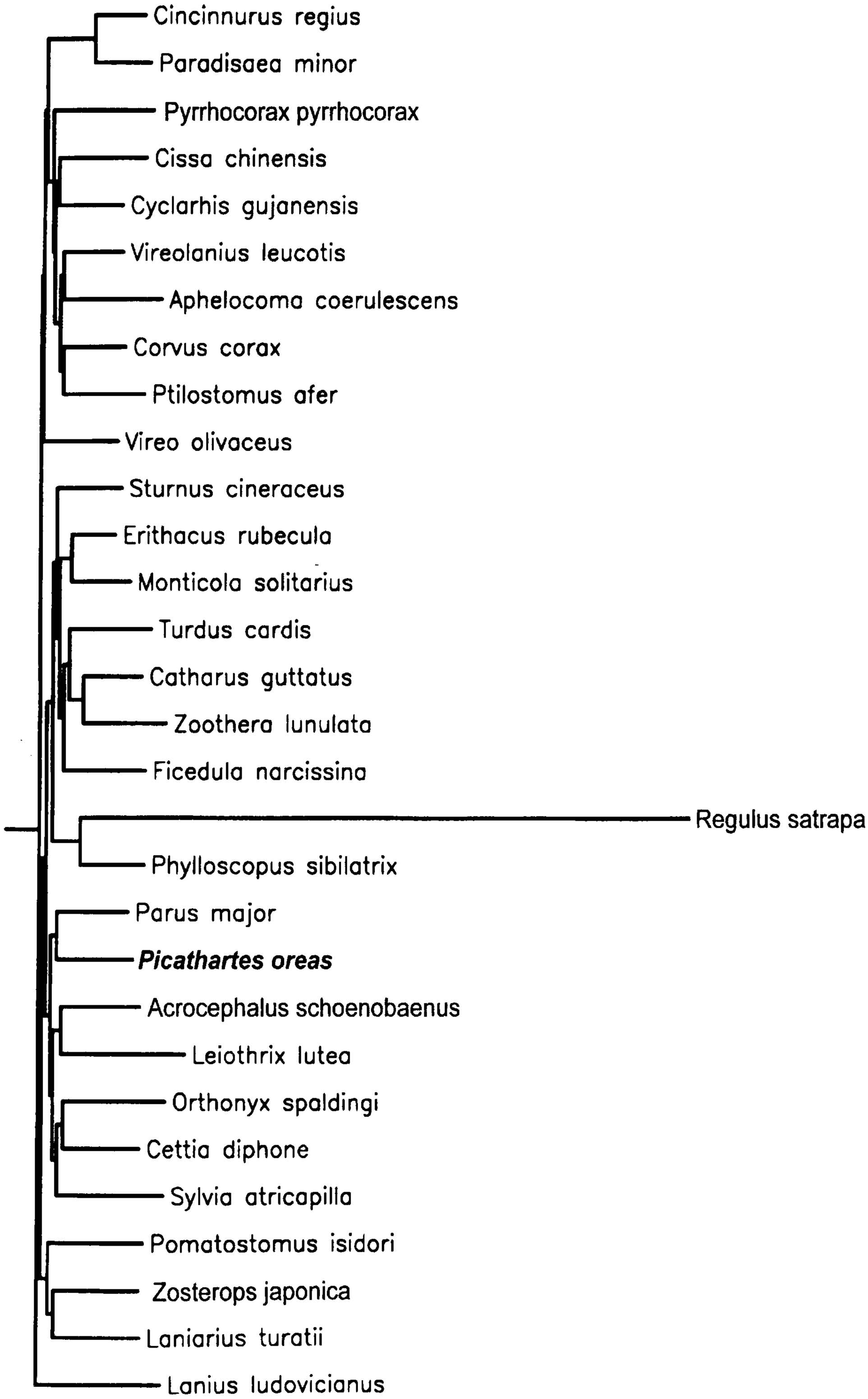
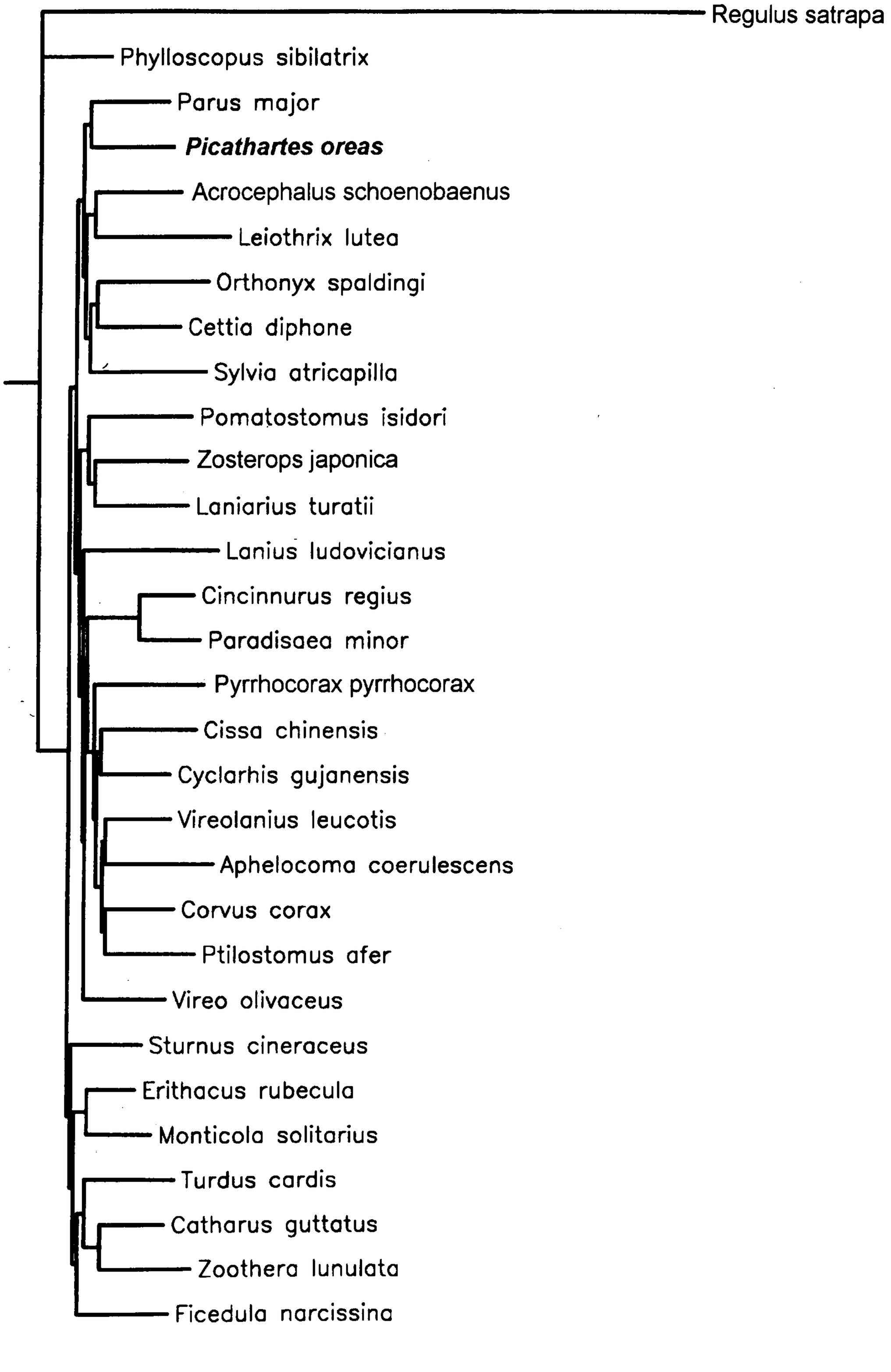


Fig. 7.5b. Fitch-Margoliash phylogenetic tree of *Picathartes* and putative relatives from 29 taxa. Correction for multiple hits based on Felsenstein's DNAML model. *Regulus satrapa* used as outgroup.



Distance-based analysis

Fig 7.5 shows Fitch-Margoliash distance trees based on estimated total sequence divergence corrected for multiple hits on the basis of Felsensteins DNAML model (see Section 7.3.4). *Lanius ludovicianus* and *Regulus satrapa* are used as outgroups in Figs 7.5a and 7.5b respectively. A total of 23,645 trees were examined by the Fitch-Margoliash program before production of Fig 7.5. The average percent standard deviation (optimality criterion for this program) is 7.4563.

In Fig 7.5a, a corvid clade (*Cincinnurus* to *Ptilostomus*) and a thrush assemblage (*Sturnus* to *Ficedula*) are clearly recognisable.They are separated by *Regulus* and *Phylloscopus* from a heterogenous grouping comprising *Picathartes*, the Paridae, Sylviidae, Zosteropidae, Timaliidae, Orthonychidae and Laniidae. Fig 7.5b is similar, except that *Lanius ludovicianus* joins the corvid clade.

7.5. Discussion

7.5.1. Methodology

Wright (1997) likened searching for the "best" phylogenetic tree to trying to hill-climb in the mist. The "best" tree is analogous with the "true" peak. With "difficult" datasets, subpeaks may be mistaken for the true peak. The data analysed here may be considered a difficult dataset, as the sequences were of significantly different lengths (Appendix 7.2), making alignment more difficult and also because some of the species may not have been closely related.

The accuracy of phylogenetic trees is evaluated by an optimality criterion. This differs between tree construction methods eg log likelihood for DNAML and average percent standard deviation for Fitch-Margoliash. Many phylogenetic tree building programs search for the "best" tree by rearranging a starting tree in a prespecified way, then calculating the optimality criterion. If a rearrangement has been successful ie the optimality criterion has improved, the tree is rearranged, a new optimality criterion

determined and so on. The process stops when no rearrangement improves the optimality criterion. To check that this is the "best" tree, it is best to restart the whole process with a different initial tree arrangement and see if the final tree has an improved optimality criterion (Wright, 1997).

The PHYLIP programs used in this analysis search for the "best" tree by a method which has three components:

a) Local rearrangements of the tree - this is automatic and prevents the tree search getting stuck on an obvious subpeak

b) Global rearrangements - ensures that a bigger peak anywhere nearby is not missed but slows down the programs by a factor of three.

c) Multiple Jumbles - starts the search process from different starting trees a prespecified number of times. This slows down the programs many times over but ensures that the input order of species to the program does not influence the starting tree arrangement and hence the final tree.

Global rearrangements and Multiple Jumbles are both optional but they were both invoked in this analysis (Section 7.3.4). This improved the validity of the trees obtained. However, several other methodological factors may have influenced results. First, the length of *Picathartes* sequence used for comparison with other taxa was 325 base pairs.The cytochrome *b* gene is at least 1143 base pairs long (Edwards and Wilson, 1990). Variation in estimates of genetic distance increases as the length of homologous DNA compared decreases because the sampling scheme is non-random, being entirely dependent on the choice of primers used (Martin *et al*, 1990). Second, some assumptions underlying the analysis may not have been optimal. Phylogenetic trees are outgroup-sensitive. Trying different outgroups and comparing optimality criteria of the different trees obtained may improve the "best-fit" tree. Also, DNAML and FITCH assume the basic model of evolution which includes the assumption of no between-sites variation in the rate of evolution. If codon positions vary in evolutionary rate in the dataset, then phylogenetic trees produced from such data can be optimised by determining the approximate ratio of variation between sites, from distance values, and incorporating this information in the programs by invoking the

"rates" option. This option was not invoked in this analysis because of lack of time. Finally, the strength of the cladistic signal from the Fitch-Margoliash method could have been evaluated by bootstrapping the distance values obtained from DNADIST, then using the bootstrapped data to construct strict consensus trees (Felsenstein, 1985; Wright, 1997). But results from bootstrapping are difficult to interpret statistically, because its underlying assumptions are rarely, if ever, satisfied by data such as coding DNA (Helm-Bychowski and Cracraft, 1993). The method was therefore not used, as it is also extremely CPU time-intensive.

7.5.2. Taxonomic relations of *Picathartes*

Some common patterns can be discerned in the phylogenetic trees produced in this analysis. The Paradiseidae, Corvidae and Vireonidae always occurred together (Figs 7.3 - 7.5). The thrushes, starling and flycatcher formed another consistent group in all the trees, with the babblers *Pomatostomus* and *Leiothrix* occurring in this group in the maximum likelihood trees. *Regulus satrapa* and *Phylloscopus sibilatrix* occurred together in all the trees. Grouping and relative position among the remaining taxa was less consistent but *Parus*, *Zosterops* and *Sylvia* occurred together in the maximum likelihood trees.

Although there are some inconsistencies, these patterns largely agree with previous work. The thrushes (Turdinae), babblers (Timaliinae or Timaliini) and flycatchers (Muscicapinae) are generally recognized by traditionalists and DNA systematists alike, as forming a loosely related assemblage (eg Sibley and Munro, 1990; del Hoyo *et al*, 1992). Sibley and Munro (1990) proposed that the starlings (tribe Sturnini) are related to the thrushes rather than the crows as traditionally treated (eg Voous, 1977; Howard and Moore, 1991). The consistent grouping of *Sturnus cineraceus* with the thrushes in this analysis supports Sibley and Munro (1990). The clustering of the crows, jays, birds-of-paradise, vireos and peppershrikes in all the phylogenetic trees, and also with *Orthonyx, Lanius and Pomatostomus* in maximum likelihood analysis agrees with Sibley and Munro's (1990) treatment of these taxa as one superfamily, the Corvoidea. *Parus, Sylvia* and *Zosterops*, which occur together in the maximum

likelihood trees, are also treated as belonging to one superfamily - Sylvioidea - by Sibley and Munro (1990).

In the past, *Picathartes* has been most frequently placed in or close to the Corvidae, or with the babblers (Timaliidae or Timaliini)(See Section 7.2). Sibley and Ahlquist (1990) placed *Picathartes* on the boundary between the parvorders Corvida and Passerida. The Passerida includes the Muscicapidae, Sturnidae, Paridae, Sylviidae and Timaliini ie the traditional thrush-babbler assemblage among others, while the Corvida contains corvine taxa such as crows, jays and birds-of-paradise, as well as the vireos, logrunners, true shrikes and australo-papuan babblers and several other families (see Sibley and Ahlquist, 1986; Sibley *et al*, 1988; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990).

In this analysis, there were two common characteristics of the relative position of *Picathartes* in all the phylogenetic trees:

a) *Picathartes* never occurred in the same clade as the members of the Corvida which consistently occurred together ie crows, jays, birds-of-paradise, vireos and peppershrikes

b) *Picathartes* always occurred next to the small group formed by *Regulus satrapa* (Sylviidae or Regulidae) and *Phylloscopus sibilatrix* (Sylviidae) which was present in all trees.

In the maximum likelihood trees, *Picathartes* occurred by itself as one of the five main branches in Fig 7.3 but in Fig 7.4 formed part of a group made up mainly of the thrush-babbler assemblage. In Fig 7.4a & b, *Picathartes* is closest to the Logrunner, *Orthonyx spaldingi.*

In the Fitch trees, the closest taxon to *Picathartes* was *Parus* (Fig 7.5). Together, the two taxa occurred in a clade comprising Sylviidae, Timaliidae and the Logrunner, *Orthonyx.*

On balance, this analysis suggests that *Picathartes* is closer to members of the parvorder Passerida than those of the Corvida. This agrees with previous suggestions that *Picathartes* is more closely related to members of the thrush-babbler assemblage rather than to the crows (eg.Delacour and Amadon, 1951; Dowsett and Forbes-Watson, 1993). Descent from the Passerida, which evolved in Eurasia, North America and Africa is probably a more parsimonious explanation for *Picathartes* than descent from the crows which apparently evolved in Australia and New Guinea.

One inconsistency in the evidence for this inference is the apparent close relationship between *Picathartes* and *Orthonyx* produced by DNAML in Figures 7.4a & b. In Sibley and Munro's (1990) classification, *Orthonyx* is treated as a member of the Corvida. The two species of *Orthonyx* occur in New Guinea and eastern Australia and there are many uncertainties about their taxonomic relationships. They have been assigned to various families, most often to the Timaliidae or the Orthonychidae, usually accompanied by several genera of uncertain affinities. *Orthonyx*, like *Picathartes*, has clearly been a taxonomic puzzle (Sibley and Ahlquist, 1990). This raises the possibility that DNAML assigned the two taxa to positions close to each other simply because they did not fit in anywhere else.

However, it should be noted that *Orthonyx* and *Pomatostomus* were until recently, frequently classified as babblers (Timaliidae)(eg Campbell and Lack, 1985) and were removed to the parvorder Corvida by Sibley and Munro (1990). In this analysis, these two taxa tended to occur with the groups containing thrushes and babblers (Figs 7.3 - 7.5).

Picathartes occurs next to *Parus* in the FITCH trees. The Paridae are known to be related to the Sylviidae and Timaliidae, both groups to which *Picathartes* has been previously assigned (Sibley, 1998; Dowsett and Forbes-Watson, 1993). Also, Dowsett and Forbes-Watson (1993) position *Picathartes* between the Timaliidae and Paridae, in their checklist of birds of the Afrotropical and Malagasy region (Fig 7.1). However, FITCH is known to perform less well than maximum likelihood in the construction of phylogenetic trees (Wright, 1997).

DNA sequences for genera that have been previously suggested as the closest relatives of *Picathartes*, notably *Eupetes* (Serle, 1952; Olson, 1979), *Turdoides* (Sibley, 1973) and *Chaetops* (Sibley and Munro, 1990), were not available in genebanks for inclusion in this analysis. When these data become available, it will be possible to move further toward resolving the taxonomic relationships of *Picathartes*. Also, more extensive molecular analysis work, beyond the scope of this thesis, could involve the design and use of specific primers for elucidation of the cytochrome *b* gene of *Picathartes*. This would further help to improve the accuracy of phylogenetic trees constructed to determine the affinites of Picathartes.

At present, my analysis suggests that *Picathartes* is more closely related to the Passerida than the Corvida. This is contrary to the tentative conclusions of Sibley and Ahlquist (1990) that *Picathartes* is a member of the Corvida but agrees with the traditional views of Delacour and Amadon (1951) and Dowsett and Forbes-Watson (1993) that the taxon is related to the thrush-babbler assemblage. I suggest, in accordance with Brosset (1965) and Sibley and Ahlquist (1990) that *Picathartes* may well be a relict of an archaic avian order as depicted in Fig 7.3.

CHAPTER EIGHT

RECOMMENDATIONS FOR CONSERVATION AND MANAGEMENT

In this chapter, I discuss the implications of the main findings of the thesis for the conservation and management of *Picathartes* populations.

Picathartes is sexually monomorphic in terms of plumage. In Chapter Three, I show that males are larger than females and that this can be detected in the field by taking tarsal measurements. This information can be used to sex individuals in any research, management or conservation programme.

Breeding success of *P.gymnocephalus* (proportion of eggs producing young) was 22.9% and productivity was 0.22 chicks fledged per adult. One of the reasons for nest losses was infanticide (Chapter Three). I suggest that infanticidal behaviour in *Picathartes* colonies is a consequence of competition for limited nest sites and that this may mainly be due to non-breeding floaters (Chapters Three and Six). If breeding success is being limited by nest-site availability, providing extra nesting surfaces in the vicinity of existing nest sites may be a practical means of improving productivity. Such "supplementary sites" should as far as possible be created with natural materials from the forest and have structural features within the range of the criteria determined for existing *Picathartes* sites in Chapter Six.

The low primary productivity of *Picathartes gymnocephalus* populations in Sierra Leone means that annual adult survival is almost certainly more than the 87% used in the population dynamics model in Chapter Three. This follows from data presented in Chapter Six, which shows that although *Picathartes* population density is low (0.46 individuals km^{-2}) and populations are small, such small populations have existed in Sierra Leone for a long time (records now cover a period of almost a century). Populations are therefore either declining very slowly or not declining at all. This is contrary to the present widely-held view (see Collar *et al*, 1994). More information is

required in this area and a follow-up study, using marked birds is recommended. This would provide data on those aspects of the species' breeding parameters and population dynamics which are still lacking (eg age at first breeding; age-specific fecundity), and would enable a more complete analysis of the population dynamics of the species to be carried out. As Green and Hirons (1991) point out, the investment of research effort into the study of the ecological requirements and breeding success of a species with a small but stable population frequently reduces the time taken to identify the causes of any subsequent decline. The results of this thesis provide a good framework for any follow-up *Picathartes* research. A total of 37 marked birds now exist at one nesting site; birds can be sexed in the field; handling and trapping methods have been perfected and appropriate equipment is available in-country. Research effort investment would be relatively minimal to acheive the stated objectives.

Protection of nesting sites within forest reserves, where unlicensed exploitation is illegal, may be possible through cooperation with local people. Because of traditional links between nesting sites and local custom (Allport *et al*, 1989; Kandeh and Richards, 1996), local people were very receptive to the idea of protecting *Picathartes* nesting sites during this study. I propose a sytem in which Government Wildlife Rangers work with designated local "site wardens" to protect large known nesting sites (eg Baiama and Komende in the Kambui Hills; Lower Koye in the Gola forest; Appendix 6.3). Site wardens appointed with the knowledge and consent of local people would report on activity in and around nesting sites to wildlife rangers, who in turn could take protective action if required. Government wildlife rangers are few, and usually based in large towns away from nesting sites; this system would increase their effectiveness and ensure cooperation with local people. The problem would be how to finance "site wardens" on a long term basis. In this study, the system worked very well in ensuring study sites were not disturbed by human activity, because site wardens were paid by the project. A system to ensure long-term cooperation needs to be worked out.

The locations of the largest nesting sites in the various regions of Sierra Leone will be extracted from the data in Chapter Six (Appendix 6.3.) and presented to the Ministry of Agriculture and Forestry in Sierra Leone for incorporation into management plans for the forest reserves in which they occur. This has already been done with regard to the Gola forest, using initial results from this study and that of Allport *et al* (1989)(see Iles *et al*, 1993). The interim management plan for Gola forest now contains an area of "high wildlife interest" which includes the largest known *Picathartes* nesting site in the forest. In the context of the plan, this area would be excluded from logging and other human activity. Most of the forest reserves in Sierra Leone where *Picathartes* occurs, do not yet have management plans (Davies and Palmer, 1991), so this is an opportune time for such an initiative.

The Gola forest is presently the most important forest reserve for *Picathartes gymnocephalus* in Sierra Leone. It holds the largest known numbers of nesting sites and the ratios of active to abandoned colonies, is higher than in any of the other surveyed forests(Chapter Six). This reinforces previous recognition of the forest as a priority area for conservation in the Upper Guinea forest block (Phillipson, 1978; Roth and Merz, 1983; Davies, 1987; Allport et al, 1989; Stuart and Adams, 1991; Cole, 1996). Speedy resumption of the Gola Rain Forest Conservation Programme (see Chapter Two) , as soon as security conditions allow, is clearly essential. A search for the large colony of *P. gymnocephalus* reported by J. Wools (Chapter Six) in the Tama-Tonkoli forest is also recommended.

Little is presently known of the distribution and abundance of *Picathartes gymnocephalus* in its other range states of Guinea, Liberia, Cote d'Ivoire and Ghana. Previous records from Guinea and Cote d'Ivoire are few and Guinea may have relatively little suitable habitat (Collar *et al*, 1994, Hayman *et al*, 1995). The species was reported to be fairly widely distributed in Liberia until the early 1980s (Collar and Stuart, 1985) but there has been no information on its status for almost two decades, including a period of civil war. An assessment is urgently required now that the war has ended. There were several records of *gymnocephalus* from Ghana into the 1960s (McArdle, 1958; Grimes and Gardiner, 1963; Grimes and Darku, 1968; King, 1979)

and the known population was thought to be of the order 200-300 pairs (King, 1979). However, there have not been any published records since the 1980s and an ongoing survey to identify important bird areas throughout the country has so far not located the species (P. Wood, pers. comm.). It would be particularly useful to try to relocate the colonies studied by Grimes and Darku (1968) and to determine breeding success at these sites. This would provide data on productivity changes (if any) after about 30 years and help to explain the difference between the breeding success levels obtained in this study (Chapter Three) and those obtained by Grimes and Darku (1968). In summary, Sierra Leone now has the most comprehensive and up to date information on the distribution and abundance of *P. gymnocephalus,* in any of its range states. The species may therefore stand its best chance of benefitting from a country-wide conservation management programme here. A means of implementing such a programme already exists in the form of the Gola Rain forest Conservation Programme. The main obstacle to its implementation in the near future is political instability and the resulting poor security.

One important point which has emerged from this study is that the population density of *gymnocephalus* is lower than that of any other threatened species for which data are available in Sierra Leone. Consequently, even the largest and most pristine forest in the country, Gola, probably has a total local population at or close to levels generally thought to be the minimum for viable populations (50-500; Stewart and Hutchings, 1996). This is consistent with findings elsewhere that *Picathartes* can exist in very small populations for long periods (Butynski *et al*, 1996). However, even if populations are presently stable, any change in environmental factors could lead to a rapid and precipitous decline. Long term monitoring of *gymnocephalus* populations in Sierra Leone is therefore strongly recommended as this will allow early detection of any changes, and permit rapid corrective action. Data on distribution and abundance of nesting sites in Chapter Six provide a baseline for such long-term monitoring. A simple system, designed along the lines used in this study, in which trained assistants check nest contents at prespecified intervals at selected nesting sites, would provide long-term records on productivity and population trends.

There is a clear association between habitat degradation and the abandonment of *gymnocephalus* colonies (Chapter Six). Colonies in non-forest vegetation are more likely to be abandoned than colonies in forest; and the forest surrounding active colonies was of better quality than that at abandoned colonies. However, *Picathartes* was for the first time recorded breeding in cultivated vegetation. Also, several active nesting sites both in Sierra Leone and Cameroon were very close to areas of high human activity (footpaths and roads, farms, fruit gardens, a charcoal-burning pit and tree-felling clearings). It is clear that *Picathartes* can be very tolerant to disturbance. This may mean that habitat fragmentation does not pose as serious a threat to the birds as would have been expected. Birds probably make regular use of clearings and other non-forested habitat in their daily activities. Fears that colonies in forest patches may be prone to local extinction primarily because birds will not disperse across non-forested areas (Allport *et al*, 1989), are almost certainly groundless. Also, high tolerance to disturbance may mean that *gymnocephalus* colonies in community forests around settlements may survive, if colonies are not directly disturbed and sufficient suitable habitat for foraging remains. Negotiations with local authorities and use of site wardens may result in protection of such colonies wherever this is possible.

Contrary to published accounts (Collar and Stuart, 1985; Allport *et al*, 1989, Ausden and Wood, 1991), *Picathartes* is protected by law in Sierra Leone (see Chapter One). These laws (the Wildlife Conservation Act of 1972) are now being revised to upgrade outdated deterrents (pers. comm. with P. D. Palmer, Chief Conservator of Forests in Sierra Leone). But the key to their effectiveness will be enforcement on the part of the Government and awareness on the part of local communities, that these laws exist and to which animals they apply. Extensive upgrading and rehabilitation of the Government Wildlife Conservation Branch and widespread local community education and participation would be important components of any process to resolve these problems. There are now several non-governmental conservation organisations in the country (e.g. Conservation Society of Sierra Leone) which could play a significant role in community education and bridging the gap between Government authorities and local communities.

In the long run, survival of *Picathartes* populations in Sierra Leone will depend on the continued existence and proper management of the forest reserves in which they occur. Numerous recommendations towards this end have been made over the last three decades (Wilkinson, 1974; Phillipson, 1978; Oates, 1980; Davies, 1987; Allport *et al*, 1989; Ausden and Wood, 1990; Davies and Palmer, 1991; Stuart and Adams, 1991; Iles *et al*, 1993). What is now required is action on the ground. This process has already started. Between 1990 and 1995; the first National Park (Outamba Kilimi) was declared in Sierra Leone, the Gola Rain Forest Conservation Programme was initiated and the country became a ratified signatory to CITES and the 1992 Rio biodiversity convention. The resumption and continuation of this process after a damaging civil war will depend on financing and also, trained and dedicated individuals.

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APPENDIX

Appendices for Chapter Three

Appendix 3.1. Biometrics and body weights of adult *Picathartes gymnocephalus* trapped at all study sites during study period

No	Capture Date	Site	Colour rings	Weight (g)	Lengths (mm): Wing	Bill	Tarsus	Tail	Retrap status
1	5.11.90	Gola	r w ;	238	167	33	65	205	New
2	5.11.90	Gola	r b;	216	170	34	72	185	New
3	5.11.90	Gola	; r dbl	204	159	33	72	176	New
4	22.7.92	Kambui	w y ;	220	163	32	75	185	New
5	22.7.92	Kambui	w r ;	218	164	30	75	180	New
6	20.8.92	Kambui	; bl y	214	156	nr	nr	nr	New
7	20.8.92	Kambui	w bl;	212	nr	nr	nr	nr	New
8	8.11.92	Kambui	g r; w	200	172	nr	nr	nr	New
9	26.11.92	Gola	w bl; y	217	160	34	60	190	New
10	26.11.92	Gola	o bl; g	247	155	30	62	170	New
11	5.3.93	Kambui	w r w;	215	160	nr	60	182	New
12	29.3.93	Kambui	w o w; y	218	163	35	nr	170	New
13	29.3.93	Kambui	w g w; y	230	170	35	60	190	New
14	3.4.93	Kambui	w b w; y	194	161	32	55	190	New
15	22.5.93	Kambui	w y w; y	214	162	35	50	178	New
16	22.5.93	Kambui	g r w; y	nr	155	33	55	187	New
17	6.1.94	Kambui	dbl w; r g	212	171	31.6	62.2	185	New
18	6.1.94	Kambui	b dbl; r dbl	212	152	32.3	59	nr	New
19	6.1.94	Kambui	b r; b w	201.5	157	33.9	61	176	New
20	5.8.95	WAPF	b r; r	192	163	32.5	54.6	180	New
21	23.6.96	WAPF	r w; r	240	175	32.9	59.2	191	New
22	11.8.96	WAPF	r bl; r	246	172	34.1	72.5	183	New
24	14.8.96	WAPF	bl w; g	224	171	33.9	71.1	176	New
23	14.8.96	WAPF	g r; b	254	170	34.7	71.3	185	New
25	20.9.96	WAPF	g b; r	232	162	33.7	67.8	175	New
26	20.2.93	Kambui	w y;	218	174	nr	60	182	Retrap
27	23.4.93	Kambui	; bl y	209	162	34	50	nr	Retrap
30	22.5.93	Kambui	w bl;	208	159	35	50	165	Retrap
29	20.5.93	Kambui	w o w; y	196	160	nr	56	nr	Retrap
28	20.5.93	Kambui	g r; w	207	157	35	55	180	Retrap
31	22.5.93	Kambui	w g w; y	229	175	34	50	Lost	Retrap

Key to colour rings:
r = red; g = green;bl = blue; b = black; w = white; y = yellow
o = orange;d.bl = dark blue
Letters preceding semi-colon denote rings on right leg
letters after semi-colon denote rings on left leg
nr = data not recorded

Appendix 3.2. Measurements of adult *Picathartes* skins recorded at the Tring Museum

No.	Collection date	Site	Sex	Body measurements (mm): Bill	Wing	Tail	Tarsus
P. oreas							
1	28/11/49	Mt. Kupe	F	35.05	158.0	160.0	44.9
2	27/8/49	Mamfe	M	38.7	160	164	45.7
3	27/8/49	Mamfe	M	38.0	165	156	51.0
4	11/3/51	Mamfe	M	38	164	155	50.0
5	?/?/02	Efulen	M	35.0	157.0	156.0	47.7
6	27/8/49	Mamfe	M	37	156.0	160.0	52.0
7	27/8/49	Mamfe	F	34.0	157.0	159.0	45.0
8	27/1/02	Efulen	F	34.0	148	146.0	46.0
9	23/7/57	Victoria	F	39.0	nr	nr	49.0
10	27/8/49	Mamfe	F	38.5	162.0	156.0	48.0
11	15/1/02	Efulen	F	32.0	149.0	142.0	44.5
12	5/7/05	Efulen	M	35.0	148.0	140.0	50.0
P. gymnocephalus							
1	18/9/50	Mongheri	F	32.5	152.0	185.0	50.0
2	8/5/68	Mt Nimba	F	30.0	158.0	193.0	47.0
3	6/11/67	Mt Nimba	F	32.2	160.0	190.0	51.8
4	23/8/58	Mongheri	F	30.3	167.0	193.0	50.9
5	/4/31	Sugar Loaf	U	34.0	160.0	200.0	55.0
6	nr	Denkera	U	32.7	155.0	200.0	55.0
7	nr	Denkera	U	35.0	165.0	192.0	50.0

M = male, F=female, U=unknown sex
nr = measurement not recorded to avoid damage to skin or information not available.

Appendix 3.3. Measurements of *Picathartes gymnocephalus* nests (cm)

Region	Site	Nest No.	Nest dimensions (cm) Internal width (rim)	Internal length (front to back)	Internal depth	External height (front)	External height (back)	Rim
Gola	UKR-A	1	15	15.5	9.5	11		1
		2	16.5	10	12	15		0.7
		3	18	12	13	12		0.9
		4	12.5		11.4			
	UKR-B	5	19	14	14	13		0.8
		6	18.5	14		11		
	Lalehun	7	14.8	11.4	10	17		0.7
		8	16	10.8	13.5	12.5		0.7
	Lalehun-B	9	15.3	8.5	13	14.5		0.8
	Male	10	16	9	13	16		
		11	20	12	11.5	20		1
		12	18	13	11	12		1
	LKR	13	16	9.6	15	20		1
		14	15	10.4	15.8	17.7		1
		15	16.5	8.8	15	14		1
	Tanima	16	17.3	14.3	14.5	15.5	19.5	1
		17	19.7	8.3	13.5	16.8	21.5	1.5
	Njagor	18	20.3	9.3	15	19.3	21.3	0.7
		19	18.6	11.6	12.3	17.5	18.5	1.3
	Belebu	20	21.4	9.3	11.3	21	22.6	1.3
		21	18.8	10.5	12	18.1	18.7	1.3
	Perrie	22	17.3	9.3	13.3	19.4	23.3	0.6
		23	20.2	11.8	14.5	13.4	16.4	0.9
	Venima-B	24	19.3	9.3	13.3	15	21.3	1.6
Kambu	Baiama	25	16	11.5	11.8	10	20	1
		26	19	11	15	20	19.5	1
		27	19	11	10	11	19	1
		28	16.1	10	15	20	24	1.4
		29				18	15	
		30				24	26	
	Komende	31	18		10.5	21	20	1
		32				11.1	21	
		33	18			15.8	22	
		34	16.5			10	19	21
		35	16			12.3	8.5	21
		36	16				7.5	14
Loma n	K/baia-A	37	16			11		20
	K/baia-B	38	20			13	14.5	15.5
		39	17		12	13	14	16

Appendix 3.3.(cont). Measurements of *P. gymnocephalus* nests (cm)

Region	Site	Nest No.	Nest dimensions (cm) Internal width (rim)	Internal length (front to back)	Internal depth	External height (front)	External height (back)	Rim
	Sinikoro-A	40	20	10	8	6	16.5	
		41	17	10.5	10.5	11	19.5	
	Sinikoro-B	42	16	10	13	11	18	
	Sinikoro-C	43	18	11	12	14	24	
	B/karafaia	44	16	12.5	15	15.5	23	
Kangar	Nyanahun-	45	18	11	20	36.8	43.3	1.9
	Nyanahun-	46	19.57	11.4	15	23.8	27	1.6
	Moyogbo	47	18.4	12.2	4	15.7	11.5	1.8
	Lomabu-A	48	18.5	10.5	15.8	17.5	24.2	1.7
		49	11.8	4.4	11.5	14.6	16	1.4
	Kotohun -A	50	19.9	12	10.8	20.4	21.5	1.5
	Kotohun-B	51	18	10.8	13.8	9.4	23.4	1.4
Dodo	Baoma	52	9.9	6.4	7.8	8.3	7.2	0.8
	Kpogbu-A	53	17.8	11.2	11	12.4	13.2	1.4
	Kpogbu-B	54	19.4	10.4		20.8	22.6	1.9
WAPF	J-O-B:3	55	21	12	17.5	24	17	1
	J-O-B:2	56	17	13.8	10	16	9	1
	J-O-B:1	57	16	10	12	9	25	1
		58	17	10.4	18	16.5	24	1
	J-O-B:4	59	15	13	15	26	20	
	BJ	60	15	11	14	19	16	
	Ngbohnoki	61	16	11	15	25	28	
	Bennet1	62	16	10	18	24	19	
	Bennet2	63	16	10	15	19	17	
	No.2	64	15	11	13	19	16	

Appendix 3.4. Dimensions and weights of *Picathartes gymnocephalus* eggs

Site	Nest	Egg no.	Length (mm)	Breadth(mm)	Weight(g)	Date found
Gola-lkr	N4a	1	38	26	15	17/11/92
		2	42	21	13	
Gola-maleh	N4b	3	38	27		18/11/92
Gola-ukr	N2b	4	40	21		27/11/92
		5	40	20		
Kambui-b	N4	6	36.9	25.8	13.5	01/08/93
		7	37.2	26.3	13.75	
Gola-dea		8	41.1	23.7	16.5	25/08/93
Kambui-b	N7	9	40.3	26.66	16	26/08/93
		10	39.8	26.9	16.5	
Kambui-k	N7	11	40	26.5	16	30/08/93
		12	39.3	26.5	16.5	
Kambui-b	N3	13	38.7	26.2	13.55	04/09/93
		14	38.3	25.5	13	
Kambui-b	N5	15	38	25.8	13.9	06/09/93
		16	38.3	26.1	14	
Gola-lkr	N4	17	37.3	24.4	13	18/09/93
Gola-ukr	N1	18	39.8	24.3	14	19/09/93
Gola-maleh	N1	19	38	24.1	13.4	20/09/93
Kambui-b	N1	20	37.9	26.55	14.5	22/09/93
		21	38.2	26.6	13.25	
Kambui-b	N2	22	36.41	26.7	14.5	22/09/93
		23	37.7	26.5	14.75	
Kambui-b	N6	24	38.6	25.9	13.9	22/09/93
		25	37.3	25.8	12.5	
Kambui-k	N1	26	38.4	26.4	14	24/09/93
		27	40.9	25.6	14.5	
*Kambui-b	N7	28	37.6	26.5	14.75	07/10/93
*Kambui-b	N4	29	37.1	25.4	13.35	09/10/93
*Kambui-b	N4	30	36.8	24.7	13.5	10/10/93
*Kambui-b	N7	31	40.04	26.6	16.5	22/10/93
Kambui-b	N7	32	38.7	26.5	15.5	06/11/93
Kambui-b	N7	33	39.5	27.2	15	13/12/93
		34	40	27	14	
Kambui-b	N6	35	36	25.4	13	
		36	33.6	25	12	
WAPF:						
J.O.B-1	N1	37	37.8	26.8	16	23/09/94
		38	37.8	27.5	17	
J.O.B-2	N1	39	41.2	26.1	12	18/10/94
		40	39.3	25.3	11.5	
B.J-1	N2	41	38.7	28	13	04/11/94

Appendix 3.4 (cont). Dimensions and weights of *Picathartes gymnocephalus* eggs

Site	Nest	Egg no.	Length (mm)	Breadth(mm)	Weight(g)	Date found
J.O.B 1	N1	42	30.9	26.6	16	22/06/95
J.O.B 4	N1	43	38.3	27	17	
J.O.B 1	N2	44	37	26.9	16	15/07/95
J.O.B 2	N1	45	38.2	27.2	16	
	N2	46	38.2	27.3	16	
J.O.B 4	N1	47	38.3	27	17	

Missing values were not recorded

*Measurements obtained on the day of laying

Appendix 3.5. Estimated laying dates and fresh egg volumes and weights of *Picathartes gymnocephalus* eggs laid in the Kambui Hills in 1993.
Day 0 ie start of breeding season taken as July 29

Nest	Dates eggs found	Estimated laying dates	No. of days into breeding season	Egg length (l)	Egg width (b)	Observed egg weight (g)	Estimated fresh weight	Estimated mean clutch weight (g)
N4	1/8	30/7	1	36.9	25.8	13.5	14.2	14.4
			1	37.2	26.3	13.75	14.9	
N7	26/8	21/8	23	40.3	26.66	16	16.6	16.5
				39.8	26.9	16.5	16.7	
N7	30/8	27/8	29	40	26.5	16	16.3	16
				39.3	26.5	16.5	15.97	
N3	4/9	31/8	33	38.7	26.2	13.55	15.4	14.8
				38.3	25.5	13	14.4	
N5	6/9	1/9	34	38	25.8	13.9	14.6	14.7
				38.3	26.1	14	15.1	
N6	22/9	15/9	48	38.6	25.9	13.9	14.98	14.6
				37.3	25.8	12.5	14.4	
N1	22/9	19/9	52	37.9	26.55	14.5	15.5	15.5
				38.2	26.6	13.25	15.5	
N2	22/9	19/9	52	36.41	26.7	14.5	15.02	15.15
				37.7	26.5	14.75	15.3	
N1	24/9	20/9	53	38.4	26.4	14	15.5	15.5
				40.9	25.6	14.5	15.5	
N7	7/10	7/10	70	37.6	26.5	14.75	15.3	15.3
N4	9/10	9/10	72	37.1	25.4	13.35	13.9	13.3
	10/10	10/10	73	36.8	24.7	13.5	12.99	
N7	22/10	21/10	84	40.04	26.6	16.5	16.4	16.4
N7	6/11	5/11	99	38.7	26.5	15.5	15.7	15.7
N7	13/12	29/11	123	39.5	27.2	15	16.9	16.7
				40	27	14	16.89	
N6	13/12	3/12	128	36	25.4	13	13.4	12.7
				33.6	25	12	12.2	

Appendix 3.6. Weight loss by *Picathartes gymnocephalus* eggs during incubation

Days after laying	Egg weights(g): N4.1	N4.2	N3.1	N3.2	N2.1	N2.2	N4.1b	N4.2b
0							13.5	13.35
1								
2	13.75	13.5						
3	13.6	13.5				14.75	14.5	
4			13.55		13			
5	13	13						
6	13	13	13.5		13			
7	13	12.8				14.25	14	
8			13		12			
9							13	
10						14	14	13	13
11							13	12.8
12						14	14	13	12.75
13								12.9	12.75
14									12.75
15	12.35	12.3						12	
16						13.5	13.5	12	12
17						13.5	13.5	12	12
18						13	13.1	12	12
19								12	
20						12.5	12.75		

Appendix 3.7. Quantitative parameters of the incubation behaviour of *Picathartes gymnocephalus*

Date	Nest	No. eggs	Egg age (dys)	Time of day (hours)	Duration of obser-vations	Time bird in nest (hrs)	Time bird in nest (%)	Mean stint duration (mins)	No. of stints	Mean stint interval (mins)	Mean bout duration (mins)	No. of bouts	No. of days into breeding season	Clutch success	No. of aggressive acts	% time nest unattended
1990																
28/8	WN3	2	7	10-13.45	3.75	2.53	67.47	9.5	16	2.36	16.5	2	89	1H;1L	0	13.3
4/09	WN3	2	14	15-18.00	3	1.18	39.33	11.8	6	14.8	-	-	96	1H;1L	0	34
7/09	WN3	2	17	13-16.00	3	0.8	26.67	8	6	12.4	-	-	99	1H;1L	0	27
8/9	WN3	2	18	15.40-17.40	2	1.78	89	26.75	4	3.67	51	1	100	1H;1L	0	9
11/9	WN3	1	21	13.40-16.00	2.33	0.57	24.46	8.5	4	20.3	30	3	103	1H;1L	0	24.9
3/7	WN1	1	9	8.30-16.30	7.5	1.13	15.07	4	17	22	-	-	33	L	0	16.7
8/7	WN1	1	13	8.30-17.00	8.5	6.4	75.29	21.4	18	6.3	49	4	38	L	0	11.3
28/8	WN2	2	15	10-13.45	3.75	0.32	8.53	3.8	5	36.2	-	-	89	1H;1L	0	0
1992																
29/10	KN2	2	13	9-14.00	4.75	3.99	84	10.4	23	51.5	-	-	151	H	0	0
28/10	KN2	2	12	10-15	5	3.88	77.6	4	34	2.3	68	2	150	H	0	0
27/10	KN2	2	11	10.45-15.30	4.75	0.5	10.53	1.87	16	4.86	-	-	149	H	6	4.63
27/10	KN1	1	6	10.45-15.30	4.75	0.82	17.26	4.08	12	11.5	-	-	149	L	3	-
11/10	KN1	1	2	10-14.00	4	1.12	28	3.94	17	10.3	-	-	133	L	0	0
28/10	KN1	1	7	10-15.00	5	2.68	53.6	23	7	7.8	-	-	151	L	0	-
29/10	KN1	1	8	9-14.00	4.75	3.175	66.84	11.2	17	5.03	-	-	152	L	0	0
17/9	KN1	2	2	9-16.30	7.5	3.95	52.67	8.43	28	5.92	146	2	109	L	0	0
7/10	KN7	1	1	11.45-15.00	3.25	3.16	97.23	27.14	7	2.5	-	-	129	L	0	0
8/10	KN7	1	2	10.15-14.15	4	3.65	91.25	31.2	7	3	27	1	130	L	0	0
27/9	KN6	2	u	11-14.00	3	0.72	24	5.37	8	10.14	-	-	119	L	0	0

Appendix3.7.(cont). Quantitative parameters of the incubation behaviour of *Picathartes gymnocephalus*

Date	Nest	No. eggs	Egg age (dys)	Time of day (hours)	Duration of obser-vations	Time bird in nest (hrs)	Time bird in nest (%)	Mean stint duration (mins)	No. of stints	Mean stint interval (mins)	Mean bout duration (mins)	No. of bouts	No. of days into breeding season	Clutch success	No. of aggressive acts	% time nest unattended
1992 (cont).																
23/9	KN6	2	u	10-14.00	4	2.03	50.75	10.15	12	10.48	-	-	115	L	3	-
22/9	KN6	2	u	13-17.00	4	1.8	45	5.72	18	7.67	-	-	114	L	0	0
1993																
14/8	KN4	2	19	11-14.30	3.5	2.45	70	20.98	7	7.12	96	1	75	H	0	0
6/8	KN4	2	11	8.45-13.00	4.25	3.71	87.29	20.27	11	3.37	82	1	67	H	0	0
5/8	KN4	2	10	14.30-18.00	3.5	2.84	81.14	17.02	10	4.4	59.5	2	66	H	0	0
4/8	KN4	2	9	13-18.00	5	4.32	86.4	36.99	7	3.67	-	-	65	H	0	0
2/8	KN4	2	7	9-14.00	5	1.98	39.6	7.9	15	10.39	119	1	63	H	0	0
8/10	KN2	2	18	10.15-14.15	4	2.93	73.25	14.66	12	5.64	-	-	130	H	2	0
7/10	KN2	2	17	11.45-15.00	3.25	2.43	74.47	9.125	16	3.13	22	3	129	H	0	0
27/10	KN2	2	7	11-14.00	3	1.93	64.33	6.4	18	3.7	35	2	119	H	0	0
23/9	KN2	2	3	10-14.00	4	2.46	61.5	6.15	24	3.54	-	-	115	H	0	0
22/9	KN2	2	2	13-17.00	4	2.8	70	11.2	15	4.83	-	-	114	H	0	0
22/10	KN4	2	13	10-16.23	6.38	4.68	73.35	11.7	24	1	40.25	8	144	H	0	0
21/10	KN4	2	12	10-16.30	6.5	5.05	77.69	15.95	19	2.65	23.5	4	143	H	0	0
20/10	KN4	2	11	9.30-15.00	5.5	4.5	81.82	16.9	16	0.93	32.8	5	142	H	0	0
9/9	KN7	2	u	10.30-12.30	2	1.58	79	11.85	8	1.72	-	-	101	H	0	0
8/9	KN7	2	u	12.30-16.35	4.08	2.95	72.3	22.2	8	5.68	-	-	100	H	0	0
9/9	KN3	2	10	10.30-12.30	2	0.79	39.5	2.63	18	2.64	5	1	101	H	0	0
8/9	KN3	2	9	12.30-16.35	4.08	2.145	52.57	6.77	19	5.38	-	-	100	H	0	0
23/9	KN5	2	18	10-14.00	4	2.97	74.25	10.49	17	3.25	121	1	115	H	2	0
22/9	KN5	2	17	13-17.00	4	3.64	91	21.83	10	1.92	63.5	2	114	H	0	0
9/9	KN5	2	4	10.30-12.30	2	0.72	36	7.24	6	15.35	-	-	101	H	0	0
8/9	KN5	2	3	12.30-16.35	4.08	2.58	63.24	8.59	18	3.88	154	1	100	H	0	0

Day 1 of breeding seasons, 1990 - 1993 taken as June 1; H = hatched, L = eggs lost; u = egg age unknown

Appendix 3.8a: Data on relative parental time investment in incubation by *Picathartes gymnocephalus* in the Kambui Hills

Date (observation time:hrs)	Duration of incubation stints Marked parent: *w y*	Unmarked parent
23/09/93	10.47-10.49	10.30-10.40
(4)	10.52-11.17	
	11.23-11.32	12.48-13.01
	11.32-11.33.30	13.05-13.25
	11.42-11.43	13.36-14.00
	11.44-11.48	
	11.50-11.59	
	12.01-12.06	
	12.07-12.11	
	12.11-12.13	
	12.13-12.14	
	12.15-12.41	
22/09/93	13.43.25-13.55	14.32-16.04
(4)	14.17-14.24.30	
	14.27-14.29	16.41-17.00
	16.04-16.21	
	16.21-16.39	
09/09/93	11.50-11.52	10.30-10.46
(2)	12.00-12.03	
	12.04-12.10	
	12.10.15-12.23	
	12.27-12.30	
08/09/93	15.25-15.40	12.54-13.07
(4.08)	15.43.15-15.44.0	13.13-13.22
	15.52-15.52	13.25-14.05
	15.53-15.53	14.10-14.35
	15.54-15.54	14.37-14.38
	16.06-16.07	14.43-15.20
	16.07-16.09	
	16.10-16.13	
	16.30-16.35	

Appendix 3.8b: Data on relative time investment in nestling care by *Picathartes gymnocephalus* in the Kambui Hills (N5)

Date (observation time:hrs)	Duration of brooding stints (hours): Marked parent *w y*	Unmarked parent
27/9/93 (3)	11.38-11.40	11.10-11.21
	11.52-11.53	11.23-11.38
	12.14-12.19	11.55-11.57
	12.20-12.21	11.57-12.10
	12.23-12.26	
	12.36-12.38	
	12.39-12.54	
	13 .03 - 13 . 04	
29/9/93 (4)	9.32-9.33	9.41-9.51
	9.38-9.39	9.53-10.03
	10.24-10.25	11.01-11.04
	10.31-10.36	11.05-11.11
	10.39-10.46	
	10.48-10.58	
	11.11-11.13	11.33-11.50
	11.22-11.25	
	11.27-11.28	
7/10/93 (3.25)	14.13-14.31	12-12.03
		12.19-12.23
		12.29-12.31
		13.20-13.25
		13.33-14.04
8/10/93 (4)	11.45-11.50	11.03-11.27
	11.50-11.53	
		11.59-12.04
	12.21-12.25	12.04-12.17
		12.19-12.21
		13.02-13.20
		13.40-13.49

Appendix 3.9: Data from observations on parental care by *Picathartes gymnocephalus*

Date	No. of nest-lings	Nest	Nest-ling age (days)	No. of days into breeding season	Time of day (hrs)	Duration of obser-vations (hrs)	Time bird in nest (hrs)	Time bird in nest (%)	No.of stints	Mean stint duration (mins)	Mean stint interval (mins)	No. of stint intervals	No. of feeds	No.of aggressive acts	% time nest unattended
1992:															
27/10	1	KN3	u	149	10.45-15.30	4.75	0	0	-	-	-	-	9	0	-
28/10	1	KN3	u	150	10.08-15.08	4.4	0	0	-	-	-	-	13	2	-
29/10	1	KN3	u	151	9.00 - 14.00	5	0	0	-	-	-	-	6	0	-
6/11	1	KN6	u	159	9.00-15.00	5.4	0	0	-	-	-	-	8	3	-
6/11	2	KN2	0	159	9.00-15.00	5.4	3.9	72.2	24	9.75	3.55	22	2	0	0
7/11	1	KN6	u	160	9.45-13.45	4	0	0	-	-	-	-	5	0	-
7/11	2	KN2	1	160	9.45-13.45	4	3	75	19	9.47	2.67	18	10	0	0
8/11	1	KN6	u	161	14.30-18.00	3.5	0	0	-	-	-	-	4	1	0
8/11	2	KN2	2	161	14.30-18	3.5	1.97	56.3	17	6.95	4.13	15	9	0	-
9/11	1	KN6	u	162	8.30-13.00	4.5	0	0	-	-	-	-	7	1	0
11/11	1	KN6	u	164	9.00-14.00	5	0	0	-	-	-	-	7	3	0
12/11	1	KN6	u	165	14.15-17.45	3.5	0	0	-	-	-	-	5	2	-
13/11	1	KN6	u	166	8.15-13.15	5	0	0	-	-	-	-	14	0	-
17/11	1	GN1	u	170	12.15-16.00	3.75	0.13	41.5	3	2.7	59	3	5	1	0
18/11	1	GN1	u	171	9.00-12.15	3.25	0	0	-	-	-	-	4	2	0
18/11	1	GN2	0	171	9.00-12.15	3.25	2.1	64.6	6	21	7.2	5	0	0	0
19/11	1	GN1	u	172	10.00-16.00	6	0	0	-	-	-	-	10	1	0
19/11	2	GN2	1	172	10.00-16.00	6	3.38	56.3	19	10.67	8.06	18	13	0	0
20/11	2	GN2	2	173	13.30-15.48	2.3	1.6	69.6	6	16	5.6	5	6	0	0
20/11	1	GN1	u	173	13.30-15.48	2.3	0	0	-	-	-	-	5	0	0
21/11	2	GN2	3	174	9.00-12.30	2.75	1.08	39.3	11	5.89	4.3	9	5	0	12.7

Appendix 3.9 (cont): Data from observations on parental care by *Picathartes gymnocephalus*

Date	No. of nest-lings	Nest	Nest-ling age (days)	No. of days into breeding season	Time of day (hrs)	Duration of obser-vations (hrs)	Time bird in nest (hrs)	Time bird in nest (%)	No.of stints	Mean stint duration (mins)	Mean stint interval (mins)	No. of stint intervals	No. of feeds	No.of aggressive acts	% time nest unattended
21/11	1	GN1	u	174	9.00-12.30	2.75	0	0	-	-	-	-	4	0	0
26/11	1	GN1	u	179	9.10-12.10	3	0	0	-	-	-	-	2	1	19
26/11	2	GN2	8	179	9.10-12.10	3	0.63	21	4	9.45	17.67	3	8	0	0
27/11	2	GN2	9	180	9.30-15.00	5.5	0.68	12.36	4	10.2	67.33	3	15	0	0
27/11	1	GN1	u	179	9.30-15.00	5.5	0	0	-	-	-	-	6	3	13.1
1993:															
15/8	2	KN4	0	76	14.00-17.30	2.5	2.17	86.8	10	13.02	1.625	8	3	0	0
22/9	2	KN3	3	114	13.00-17.00	4	2.8	70	21	8	3.245	20	9	0	0
23/9	2	KN3	4	115	10.00-14.00	4	2.1	52.5	23	5.48	4.27	22	14	1	0
27/9	2	KN5	2	119	11.00-14.00	3	2	66.7	14	8.57	4.61	13	6	0	0
27/9	2	KN3	8	119	11.00-14.00	3	0.71	23.7	11	3.87	8.8	10	4	0	0
29/9	2	KN5	4	121	9.00-13.00	3.25	1.35	41.5	16	5.06	4.57	14	7	0	0
7/10	2	KN5	12	129	11.45-15.00	3.25	1.05	32.3	6	10.5	17.6	5	13	0	0
7/10	2	KN3	18	129	11.45-15.00	3.25	0	0	-	-	-	-	13	0	9.23
8/10	2	KN3	19	130	10.15-14.15	4	0	0	-	-	-	-	14	6	0
8/10	2	KN5	13	130	10.15-14.15	4	1.38	34.5	9	9.2	6.63	8	14	0	0
20/10	2	KN5	25	142	9.30-15.00	5.5	0	0	-	-	-	-	26	3	4.24
21/10	2	KN2	11	143	10.00-16.28	6.13	2.2	35.9	12	11	15.91	12	13	0	0
22/10	2	KN2	12	144	10.00-16.23	6.21	1.42	22.9	8	10.65	23.13	8	18	3	0
2/11	2	KN2	23	155	11.30-15.30	4	0	0	-	-	-	-	14	0	0
3/11	2	KN2	24	156	13.00-16.00	3	0	0	-	-	-	-	17	0	20
3/11	2	KN4	2	156	13.00-16.00	3	2.3	76.7	11	12.55	3.7	10	10	0	0
4/11	2	KN4	3	157	12.30-16.3(	3.75	3.02	80.5	10	18.12	4.125	8	5	0	0
4/11	2	KN2	25	157	12.30-16.3(	3.75	0	0	-	-	-	-	14	10	1.7
17/11	1	KN4	17	170	10.15-14.2:	3.02	0	0	-	-	-	-	5	0	13.8

Day 1 of breeding season = June 1; u = precise nestling ages unknown but estimated from body size and/or fledging dates where appropriate

Appendix 3.10: Relative food provisioning rates of *Picathartes gymnocephalus* parents attending nests in the Kambui Hills and Gola forest

Site & nest	Date	Duration of observation (hours)	Nestling age (days)	No. of feeds: unmarked bird	marked bird
Kambui	27/9/93	3	2	2	4
Hills	29/9/93	3	4	3	4
(N5:	7/10/93	3.25	12	6	7
two nestlings)	8/10/93	4	13	7	7
	20/10/93	5.5	25-27	13	13
Gola(UKR)	18/11/92	3.25	unknown	1	3
(N1:	19/11/92	6		5	5
one nestling)	20/11/92	2.3		2	3
	21/11/92	2.75		2	3
	26/11/92	3		1	1
	27/11/92	5.5		3	3
	Totals	41.55		45	53

Appendix 3.12a: Nesting success of *Picathartes gymnocephalus* during incubation in Sierra Leone

Site	Nest	No. of eggs observed	No. of days observed	Interval between last visit & outcome	Exposure* (egg-days)	Eggs lost
Gola,90:						
	90-u1	1	8	4	10	1
	90-u1,2	2	24	5	53	0
	90-u2	2	15	4	34	0
	90-u3	2	15	4	34	0
	90-u4	2	31	5	67	2
	90-u1b,2	1	10	5	12.5	1
	90-u1b,1	1	1	4	3	1
	90-gb1	2	14	5	33	0
	90-ld2a	1	2	6	5	1
	90-ld2a,2	1	4	3	5.5	1
	90-ld1B,1	1	1	3	2.5	1
	90-ld3b	2	1	7	9	2
Gola,92:	92-u1	2	1	15	17	0
	92-u2,1	2	1	15	17	0
	92-u2,2	2	6	2	14	0
	92-u5,1	2	1	15	17	2
	92-u5,2	2	9	0	18	2
	92-u6,1	2	1	15	17	2
	92-u6,2	2	15	2	32	1
	92-u1b	2	1	15	17	1
	92-u2,1	1	1	15	8.5	1
	92-u3	2	1	15	17	2
	92-c1	2	1	15	17	2
Kambui, 92	92-b1,1	2	18	2	38	2
	92-b1,2	1	2	2	3	1
	92-b1,3	1	6	6	9	1
	92-b2	2	19	0	38	0
	92-b3	2	18	2	38	1
	92-b4	2	2	7	11	2
	92-b7	2	21	0	42	0
Kambui, 93	93-b1	2	1	0	2	2
	93-b2	2	17	0	34	0
	93-b3	2	12	6	30	0
	93-b4,1	2	13	0	26	0
	93-b4,2	2	19	5	43	0
	93-b5	2	17	3	37	0
	93-b6,1	2	5	9	19	2

	93-b6,2	1	18	2	19	1
		1	12	2	13	1
	93-b7,1	2	11	16	38	0
	93-b7,2	1	2	0	2	1
		1	1	0	1	1
	93-b7,3	1	2	0	2	1
		1	1	0	1	1
	93-b7,4	1	1	11	6.5	1
	93-b7,5	1	10	2	11	1
		1	6	2	7	0
WAPF,90:	90-W1	1	9	5	11.5	1
		1	14	7	17.5	1
	90-w2	2	1	7	9	1
	90-w3	1	11	3	12.5	0
		1	18	7	21.5	1
	90-y	2	21	0	42	0
WAPF,94:	94-j1-1,1	2	21	0	42	0
	94-j1-1,2	2	2	17	21	0
	94-j1-2	2	1	10	12	0
	94-j2	1	16	6	19	1
		1	8	8	12	0
	94-bj1,1	2	21	0	42	0
	94-bj1,2	2	1	8	10	0
	94-bj2	1	17	0	17	1
		1	1	8	5	0
	94-n2-2	2	1	10	12	0

* A nest lost during an interval of several days was assumed to have been lost on the day at the middle of the interval

Appendix 3.12b. Nesting success of *Picathartes gymnocephalus* during the nestling period in Sierra Leone

Site	Nest	No. of nestlings observed	No. of days observed	Interval between last visit & outcome	Exposure* (nestling--days)	Nestlings lost
Gola, 90:	90-u1	2	4	2	10	2
	90-u2	1	10	4	12	1
		1	19	4	21	0
	90-u3	1	10	4	12	1
		1	19	4	21	0
	90-gb1	2	27	0	54	0
Kambui, 92	92-b2	2	2	0	4	2
	92-b3	1	3	6	6	0
	92-b6	1	17	0	17	0
	92-b7	2	2	0	4	0
Kambui, 93	93-b4,1	2	22	2	46	0
	93-b2	2	27	0	54	0
	93-b3	2	24	3	51	0
	93-b4, 2	1	3	11	8.5	1
		1	14	6	17	0
	93-b5	2	24	0	48	0
	93-b7	1	14	0	14	0
WAPF, 90	90-w2	1	1	3	2.5	1
	90-w3	1	1	4	3	1
	90-y	2	27	0	54	0
WAPF, 94	94-J1, 1	2	10	10	30	0
	94-J1, 2	1	16	6	19	0
		1	8	8	12	1
	94-J2	1	21	0	21	1
	94-bj1, 1	1	1	10	6	2
	94-bj1, 2	2	3	6	12	2
	94-n2, 2	2	1	5	7	2

Appendices for Chapter Four

Appendix 4.1. Monthly rainfall (mm) at study sites

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Daru (for Gola area)												
1980	69	51.4	23.7	133.7	148.4	217.8	171.7	308.4	326.2	313.6	230.9	182.1
1981	0.3	27.7	52	128.3	222.6	299.4	368.9	320.6	368.3	346	83.1	89.9
1982	0	7.2	26.5	185.7	258.8	446.9	403.1	334.1	270.3	188.2	131.4	0
1983	0	28	31.1	177.7	243	321.6	437.4	359.5	328.9	323	186.1	38.3
1984	0	34.9	62.4	202	172.4	344.9	343	319.9	240.2	309.8	127.7	0
1985	16.7	20.7	78.7	121.5	91.1	216.3	481.6	447.9	326	257.1	124.8	1
1986	0	26.3	58.5	104.8	206.6	213.8	332.9	394.2	318.1	397.1	127.1	0
1987	32.7	0.5	25.8	88.7	289.1	337.4	235.9	422.4	387.3	274.4	66.2	65.9
1988	0	41.4	24.8	107.9	109.7	356.2	289.9	296.6	283.3	236.4	154.7	22.5
1989	15.2	27.6	115	207.1	163.2	229.8	250	387.8	366.7	448	149.9	63.3
1990	0	0	21.3	215.8	230.8	198.8	185.7	338.8	283.3	305.6	201.9	78.4
Guma Dam (for WAPF)												
1985	0	0	7.9	6.6		627.9	1154.2	1276.2	836	264.7	120.7	4.1
1986	0	0	2.6	23.1	261.4	389.6	1674.4	1544	1045.5	374.6	41.9	1.8
1987	7	0	0.8	53.3	156.5	545.3	750.8	1485.9	811	323.6	82.9	22.6
1988	0	12.7	0	44.9	81.3	371.1	2432.1	2426.7	178.3	206.3	156.7	0
1989	0	0	21.1	25.1	69.3	286	1102.3	2024.3	632.6	335	142.4	26
1990	0	11.7	5.1	19.1	130.1	508.8	2112.3	1480.3	693.7	270	82.3	43.2
1991				8.1	142	429.5	837.7	1502.7	739.9	604	51.3	12.2
1992	0	0	0	42.2	430.8	1080.8	2123.2	2479.3	472.4	194.6	51.3	0
1993	0	14.7	14	48.8	142	592.3	1845.8	1655.8	605	222.5	156.5	
Bo (for Kambui Hills)												
1985	10.1	0	34.2	111	203.3	159.5	419.5	592	482.5	307.9	294.5	0.8
1986	0	2	32.6	41.4	222.8	254.6	329	374.3	354.4	240.8	94.8	0.8
1987	9.4	30	0.4	134.5	199.2	181.2	289.7	489.4	318.1	279.9	60.2	40
1988	0		18	59.3	131.5	303.4	459.1	571.5	403.1	275.4	66.4	
1991			26.7	53.3	168.8	265.3	354.4	738.8	361.5	337.7	87.1	
1992	0	1	1.1	204.4	373.1	399.4	448.2	752.7	489.5	280.8	131.6	0
1993	5.8	0.5	90.3	95.8	219.4	601.8	1040	1094.24	424.6	268.2	100.4	0.95
1994	22.6	6.2	30.5	62.3	202.6	359.8	385.2	498.5	504.9	144.2	94.6	21.8

Appendix 4.2a. Numbers of different taxa trapped in forest pitfall traps in the Kambui Hills, 1993

Taxon	Numbers trapped on different dates:															
	Jan 13	Feb 10	Apr 2	Apr 30	May 14	May 28	Jun 11	Jun 25	Jul 9	Jul 28	Aug11	Aug 26	Sep 14	Sep 28	Oct 26	Nov 13
Apidae	4	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Araneidae	5	6	2	0	3	5	0	2	0	1	1	0	0	1	1	2
Bufonidae	1	2	0	2	1	1	2	0	3	2	5	1	0	0	0	0
Chilopoda	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0
Coleoptera	49	159	0	14	8	80	10	16	38	44	67	13	0	2	0	1
Cul. larvae	0	0	4	0	13	3	0	0	0	0	0	0	0	0	0	0
Cul. pupae	0	0	0	0	7	6	0	0	3	0	0	0	0	0	0	1
Culicidae	0	0	12	0	1	3	0	0	0	0	0	0	0	0	0	1
Diplopoda	3	1	1	0	2	0	0	0	0	1	1	0	3	1	4	2
Diptera	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Formicidae	18	19	14	25	11	15	11	29	34	22	21	36	0	18	6	12
Hemiptera	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Insecta	27	21	19	9	13	13	0	5	0	8	9	3	0	0	0	0
Isoptera	2	20	45	57	0	25	5	13	45	10	20	0	10	4	0	0
Larvae	7	16	3	19	11	24	6	3	9	9	3	5	3	0	0	1
Lumbricidae	0	0	0	6	2	10	0	2	5	10	10	1	0	1	0	1
Notonecta	0	0	25	0	0	0	0	0	15	0	0	1	3	0	0	0
Orthoptera	0	5	0	0	3	0	0	0	0	3	2	0	0	0	0	0
Pulmonata	0	0	3	1	6	1	3	5	13	6	5	1	6	6	5	3
Unid arthropod:	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Unid pupae	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	3
Vespoidea	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Dictyoptera	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1
Trichoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals	113	253	145	134	84	188	37	75	165	119	147	61	25	33	16	28
Days	13	28	23	28	14	14	14	14	14	19	14	15	19	14	14	18
Active traps	10	10	10	10	10	10	6	10	10	10	9	6	5	6	6	5

Appendix 4.2b. Numbers of different taxa trapped in forest pitfall traps in the Kambui Hills, 1992.

Prey	Numbers trapped:										
	Jun 13	Jul 14	Jul 29	Aug 12	Aug 26	Sep 16	Oct 31	Nov 15	Nov 30	Dec 15	Dec 30
Millipedes	3	4	3	5	4	4	3	8	22	17	4
Ants	22	2	11	0	6	1	5	16	17	46	50
Termites	110	38	18	284	0	1	153	5	204	211	33
Snails	1	3	1	1	1	4	5	1	3	2	1
Crickets	0	0	2	0	0	0	0	0	1	1	25
Spiders	8	2	4	0	1	0	4	3	5	6	8
Frogs	0	0	1	0	0	0	0	1	0	1	2
bees	0	0	2	0	0	0	0	1	3	3	0
Mosquitoes	1	0	0	0	0	0	0	6	0	0	0
Beetles	6	0	0	0	0	6	0	0	2	13	0
Flies	3	0	0	0	0	0	0	0	0	0	0
Earthworms	5	9	0	0	2	2	0	0	0	0	0
Crustaceans	1	0	0	0	0	0	0	0	0	0	0
Mos. larv/pup.	1	16	0	0	0	0	19	8	0	0	0
Unid. insects	40	6	68	6	2	4	7	4	77	204	224
Unid. worms	8	1	8	4	0	0	2	0	1	0	0
Leeches	0	0	0	0	0	0	0	0	1	0	0
Centipedes	0	1	0	0	0	0	0	0	1	0	0
Unid arth.	0	1	0	0	0	0	0	1	0	6	44
Unid. larvae	0	1	2	2	5	8	11	0	0	3	3
Butt.pupa	0	0	0	0	0	0	0	0	0	0	
Ins.larvae	0	0	0	0	0	0	0	0	0	1	1
Totals	209	84	120	302	21	30	209	54	337	514	395
Traps	10	8	9	7	9	7	9	8	10	10	10
Days	14	13	14	13	13	20	30	14	14	14	14

Appendix 4.3. Numbers of organisms trapped in farmbush pitfall traps in the Kambui Hills, 1993

Group	Numbers trapped on different dates:															
	Jan 13	Feb 10	Apr 2	Apr 30	May 14	May 28	Jun11	Jun25	Jul9	Jul28	Aug11	Aug26	Sep14	Sep28	Oct26	Nov13
Apidae		2	0	0	0	0		0	0	0	0	0	0	0	0	0
Araneidae		9	1	1	1	0		2	0	0	1	0	1	0	0	0
Bufonidae		2	0	0	0	2		0	5	1	2	0	0	0	0	0
Chilopoda		1	0	3	4	0		0	5	0	0	0	0	2	0	0
Coleoptera		14	4	7	16	61		8	7	37	29	3	1	0	1	3
Cul. larvae		0	0	0	46	0		14	11	321	0	1	3	0	0	0
Cul. pupae		0	0	0	0	0		0	41	0	0	4	0	0	0	0
Culicidae		0	0	0	0	0		0	0	0	0	4	0	0	0	0
Diplopoda		1	0	3	3	3		2	4	0	3	0	0	1	2	3
Diptera		0	0	0	1	0		0	0	0	0	0	0	0	0	0
Formicidae		176	4	30	89	71		6	27	43	22	9	6	0	4	6
Hemiptera		0	0	0	0	1		0	0	0	0	0	0	0	0	0
Insecta		97	10	0	30	0		3	1	15	0	3	2	0	0	0
Isoptera		3	2	14	151	15		6	42	18	13	1	1	0	0	0
Larvae		6	1	4	27	4		0	5	13	16	0	4	0	0	0
Lumbricidae		0	0	3	3	7		0	10	1	9	1	0	0	0	0
Notonecta		0	0	0	0	3		0	0	0	0	2	4	0	0	0
Orthoptera		28	0	0	2	0		0	0	0	1	0	0	0	1	0
Pulmonata		0	0	4	0	0		0	2	2	0	5	0	3	2	5
Unid arthropods		0	0	2	0	0		0	0	0	0	0	0	0	0	0
Unid pupae		0	0	0	0	0		0	0	0	0	0	0	0	0	0
Vespoidea		0	0	0	0	0		0	0	0	0	0	0	0	0	0
Dictyoptera		0	0	0	0	0		0	0	0	0	0	0	0	0	0
Trichoptera		0	0	0	0	0		0	0	0	0	0	0	0	0	0
Hirudinae		1	0	0	0	0		0	0	0	0	0	0	0	0	0
Isopoda		3	0	0	0	0		0	0	0	0	0	0	0	0	0
Unid worms		3	0	0	0	0		0	0	0	0	0	0	0	0	0
Totals	0	346	22	71	373	167	0	41	160	451	96	33	22	6	10	17
Days		28	23	28	14	14		14	14	19	14	15	19	14	14	18
Active traps		10	6	9	10	10		7	9	10	10	7	6	3	4	6

Appendix 4.4. Numbers and biomass of organisms trapped by a malaise trap operated in Kambui Hills forest from September 1992 - October 1993

Clearing date	Numbers of different taxa trapped:																		Total dry weight (g)
	Arach-nida	Lepid-optera	Isoptera	Coleop-tera	Hemip-tera	Hymen-optera	Odonata	Orthop-tera	Derm-aptera	Ephem-eroptera	Diptera	Homo-ptera	Trichop-tera	Thysan-optera	Dictyop ptera	Mecop-ptera	Psocop-tera	Isopoda	Unidentified	
Sep-30	3	5	10	19	1	33	8	23	6	1	41	0	0	0	0	0	0	0	33	4.599
0ct 30	4	35	0	31	7	48	4	0	3	0	54	0	0	0	0	0	0	0	32	1.8091
Nov-15	4	47	0	27	0	64	0	2	0	0	56	0	0	0	0	0	0	0	59	2.974
Nov-30	4	29	0	19	2	53	0	11	0	0	43	0	0	0	0	0	0	0	33	1.1188
Dec-15	1	27	0	11	0	28	1	0	0	0	54	0	0	0	0	0	0	0	45	1.4974
Dec-31	3	14	0	10	0	33	0	0	0	2	35	0	0	0	0	0	0	0	9	1.0078
Jan-15	0	30	0	18	0	19	0	3	0	0	28	0	0	0	0	0	0	0	14	2.729
Feb-10	3	70	0	5	0	58	4	10	0	1	43	1	0	0	0	0	0	0	4	1.26
Feb-24	1	65	0	4	0	294	5	0	0	0	49	2	0	0	0	0	0	0	0	1.24
Mar-10	4	35	0	11	0	41	6	7	1	0	23	0	1	4	0	0	0	0	5	1.2
Apr 30	4	21	0	16	1	53	4	2	0	0	26	0	0	0	7	0	0	0	4	1.63
May 14	2	34	0	56	1	112	9	2	0	0	37	0	0	0	8	0	0	0	5	1.63
May-28	1	12	0	10	0	37	1	5	0	0	17	0	0	0	0	0	0	0	118	0.898
June 11	2	2	0	3	2	28	2	0	0	0	8	0	0	0	0	1	0	0	0	
Jun-28	2	0	0	7	0	17	0	2	0	0	0	0	0	0	0	0	0	0	3	0.404
July 9	6	38	0	9	6	31	1	2	0	0	31	0	0	1	2	0	1	2	0	3.034
July 28	1	15	0	1	0	9	0	1	0	0	6	0	0	0	0	0	0	0	0	0.46
Aug 28	3	12	0	5	1	33	1	1	0	0	18	0	0	0	1	0	0	0	11	0.404
Sept 28	2	5	0	10	0	33	1	5	0	0	17	0	0	0	0	0	0	0	9	1.56
Oct 26	1	26	0	2	1	42	1	0	0	0	19	0	0	0	0	0	0	0	6	1.21

Appendix 4.5: Visual counts of organisms in forest undergrowth, Kambui Hills, 1992/93

Taxa	Numbers of different organisms seen on specified dates:																
	Dec12	Dec13	Jan 6	Jan7	Feb 18	Feb 19	Mar 29	Mar 31	Apr 22	Apr24	May 20	May 22	Sep 26	Sep 27	Oct 19	Nov 3	Nov 4
Agamidae	0	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Anura	5	3	2	2	1	0	1	4	0	2	0	0	5	2	2	0	0
Apidae	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0
Araneidae	40	58	58	54	33	47	38	52	36	67	70	65	29	55	34	27	34
Arthropoda	1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0
Cicadidae	0	0	0	0	2	1	1	0	0	0	0	0	0	2	0	0	20
Coleoptera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Dictyoptera	0	0	0	0	0	0	0	1	0	0	15	13	4	10	6	0	0
Diplopoda	3	8	0	0	0	1	0	0	2	8	3	3	1	3	1	0	0
Diptera	3	4	26	35	11	9	10	10	8	9	3	5	7	2	1	23	22
Formicidae	26	10	40	46	46	22	28	38	22	20	36	38	16	16	18	74	80
Gastropoda	4	6	1	0	0	0	0	3	0	1	0	0	0	0	0	0	0
Hemiptera	3	1	19	5	3	0	4	1	2	6	5	5	0	1	0	1	1
Hirudinea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Isoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caterpillars	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Odonata	0	0	4	0	16	4	3	1	2	3	3	2	1	0	3	3	3
Orthoptera	8	4	5	8	2	10	5	19	13	15	14	4	8	2	3	0	1
Scincidae	1	0	0	0	0	0	3	1	4	0	2	0	1	0	1	0	2
Unid Apterygotes	0	0	0	0	0	0	1	1	0	2	5	0	0	0	0	0	0
Unid Pterygotes	16	20	54	24	19	15	10	16	22	31	36	25	9	11	21	39	53
Psocoptera	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mantidae	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0
Chilopoda	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0
Oligochaetae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Thysanura	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Total	111	116	211	175	136	109	155	148	111	169	193	161	84	106	93	170	216
Ant columns	2	3	9	11	24	16	14	9	0	0	0	0	2	0	3	0	11
Termite concentrations	0	0	2	0	0	7	0	0	0	0	0	0	4	4	2	0	0

Appendix 4.6a: Numbers of *Picathartes gymnocephalus* clutches laid each month at different study sites in various years

Region	Year	Nos. of clutches laid:											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gola	1990	0	0	0	0	0	0	0	2	0	9	1	1
	1992	0	0	0	0	0	0	0	0	8	14	6	0
Kambui	1992	0	0	0	0	0	0	0	0	4	4	0	0
	1993	0	0	0	0	0	0	0	2	5	3	1	2
WAPF	1990			0	0	0	1	0	2	1	0	0	0
	1994	0	0	0	0	0	0	1	1	2	3	1	0
Totals		0	0	0	0	0	1	1	7	20	33	9	3

Appendix 4.6b: Numbers of *Picathartes gymnocephalus* nestlings found each month at different study sites in various years

Region	Year	Nos. of nestlings found:											
		Jan	Feb	Mar	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gola	1990							0	0	0	0	6	0
	1991	0	0	0									
	1992	0							0	0	0	5	0
	1993	0	0			0	0	0	0	2	4		
	1991			0									3
Kambui	1992	1			0	0	0	0	0	0	4	3	0
	1993	0	0	0	0	0	0	0	2	8	6	4	1
WAPF	1990	0	0	0	0	0	0	0	0	2	1	0	0
	1994	0	0	0	0	0	0	0	0	0	0	0	0
Totals		1	0	0	0	0	0	0	2	12	15	18	4

Missing data not recorded mainly because of access problems; see text.

Appendices for Chapter Five

Appendix 5.1. Prey components used as diet indicators in *Picathartes gymnocephalus* faeces. The most frequently used indicators are shown in bold type.

Taxa	Diet indicator
Coleoptera	**Mandibles**, elytra, heads, tibia
Isoptera	**Mandibles**, heads, femur, tibia
Formicidae	**Mandibles**, petioles, legs
Dermaptera	**Cerci**
Orthoptera	**Tibia**, heads, **mandibles**
Diptera	Heads, wings
Lepidoptera	Heads, wing scales
Araneae	**Fangs**, tibia and femur
Pseudosorpionida	Fangs
Other Arachnida	Pincers
Diplopoda	Segment rings, **legs** (5 legs=1 millipede)
Lumbricidae	**Chaetae** (10 chaetae = 1 worm)
Gastropoda	Whole or broken **shells**
Decapoda	**Pincers**, carapace
Anura	**Vertebrae**, tibia and femur
Lacertilia	**Scales, vertebrae**

Appendix 5.2. Data on dietary change with nestling age in the Kambui Hills 1993, obtained by direct observation

	Numbers of different prey brought to nestlings of different ages																				
Prey	Age(days):																				
	2	2	2	3	3	4	6	8	11	12	12	13	16	18	18	19	23	24	25	25	Total
Lumbricidae	0	1	1	2	2	2	0	0	6	4	7	5	7	8	3	1	4	2	3	10	68
Anura	0	0	1	0	0	0	0	1	0	0	2	1	0	1	1	0	2	0	0	2	11
Coleoptera	1	0	1	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	7
Diplopoda	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	1	1	3	0	2	11
Orthoptera	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	9
Lacertilia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	1	5
Formicidae	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	5
Araneae	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	4
Dictyoptera	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	3
Homoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2
Insect larvae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lepidoptera larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Decapoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Gastropoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Odonata																					0
Diptera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Unid insecta	1	0	0	3	2	0	0	0	1	4	0	0	0	1	2	2	1	3	3	3	26
Unid arthropoda	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3
unid prey	5	7	1	5	0	6	2	3	3	5	6	8	23	18	5	5	4	7	7	5	125
Chilopoda	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
	9	9	6	14	5	10	3	4	14	13	21	14	33	30	13	14	14	17	15	28	

Appendix 5.3. Weight - length relations of the main non-insect taxa in *Picathartes gymnocephalus* nestling diet

Earthworms		Frogs		Millipedes		Lizards	
Length (mm	Weight(g)	Length (mm	Weight(g)	Length (mm	Weight(g)	Length (mm)	Weight(g)
42	0.6955	13	0.41	17	0.05	34	1.1
62	0.3955	17	0.71	17.5	0.06	35	1.35
76	0.4925	19	0.79	25.5	0.04	42	1.5
78	0.6095	31	1.29	20	0.025	48	2.3
87	0.5125	34.5	1.25	22	0.02	52	3.2
101	1.2985	36	1.8	23	0.03	53	4.1
104	1.0355	37	2.2	30	0.11	55	4.5
109	1.1965			30	0.09	56	4.25
117	1.4215			47.5	0.17		
127	0.938			55	0.18		
136	1.551						
140	1.945						
156	1.4985						
153	2.354						
161	2.605						
165	2.5835						

Appendix 5.4. Comparison of prey occurrencies in *Picathartes gymnocephalus* nestling faeces and the relative abundance of potential prey in the environment

Taxa	Nestling faeces: % of prey occurrencies- Kambui Hills (n=689)	Pitfall traps: % of organisms in samples(p (n=240)	Visual surveys % of total (pii)	Strauss index: % diet - % in pitfall traps (r-pi)	% diet - % in visual surveys (r-pii)
Acarina	0.58	0	0	0.580551524	0.580551524
Annelida, undet.	0.29	0	0	0.290275762	0.290275762
Anura	6.39	0.93	1.18	5.456066763	5.206066763
Apidae	0.15	0.26	0.2	-0.114862119	-0.054862119
Araneae	8.27	1.31	32.3	6.962859216	-24.02714078
Chilopoda	1.74	0.52	0.12	1.221654572	1.621654572
Coleoptera	12.20	21.6	0.08	-9.4	12.12
Culicidae	0	0.61	0	-0.61	0
Decapoda (crabs)	0.44	0	0	0.435413643	0.435413643
Dermaptera	3.48	0	0	3.483309144	3.483309144
Dictyoptera	0	0.15	1.99	-0.15	-1.99
Diplopoda	3.34	1.28	1.34	2.058171263	1.998171263
Diptera	1.31	0.12	7.63	1.186240929	-6.323759071
Formicidae	11.18	22.8	23.4	-11.62438316	-12.22438316
Gastropoda	1.31	2.53	0.61	-1.223759071	0.696240929
Hemiptera	0	0.15	2.31	-0.15	-2.31
Hirudinea	0.15	0.03	0.04	0.115137881	0.105137881
Homoptera	0.00	0	1.06	0	-1.06
Insect larvae/pupa	0.87	20.21	0	-19.33917271	0.870827286
Insecta, indet.	12.92	8.36	17.71	4.557271408	-4.792728592
Isopoda	0	0.09	0	-0.09	0
Isoptera	12.19	15.2	na	-3.008417997	na
Lacertilia	1.60	0	0.81	1.596516691	0.786516691
Lepidoptera adults	0.29	0	0	0.290275762	0.290275762
Lepidoptera larva	0.29	0	0.08	0.290275762	0.210275762
Lumbricidae	12.19	2.6	0.08	9.591582003	12.111582
Nematoda	0.15	0	0	0.145137881	0.145137881
Odonata/ephemeropte	0	0	1.95	0	-1.95
Orthoptera	4.21	1.31	6.94	2.898998549	-2.731001451
Other arachnida	0.29	0	0	0.290275762	0.290275762
Other hymenoptera	0	0	0.04	0	-0.04
Pseudoscorpionida	0.29	0	0	0.290275762	0.290275762
Psocoptera	0	0	0.04	0	-0.04
Thysanura	0.44	0	0.08	0.435413643	0.355413643
arthropod, unid.	2.76	0.09	0	2.667619739	2.757619739
Vespoidea	0	0.09	0	-0.09	0
Thysanoptera	0	0	0	0	0
Trichoptera	0	0	0	0	0

na = not applicable

xxx

Appendix 5.5. Preference rank order of different taxa in *Picathartes gymnocephalus* nestling faeces

Rank order of abundance:				Differences in ranks:		
Taxa	% of prey occur-rencies in nestling faeces (n=689)	Pitfall traps % of organisms in samples (n=240)	Visual surveys % of total	Pitfall traps	Visual surveys	Average rank difference
Insecta, indet.	1.00	5	3	-4	-2	-3
Coleoptera	2.00	2	17.5	0	-15.5	-7.75
Isoptera	3.50	4	na	-0.5	na	na
Lumbricidae	3.50	6	17.5	-2.5	-14	-8.25
Formicidae	5.00	1	2	4	3	3.5
Araneae	6.00	8.5	1	-2.5	5	1.25
Anura	7.00	11	10	-4	-3	-3.5
Orthoptera	8.00	8.5	5	-0.5	3	1.25
Dermaptera	9.00	30	31	-21	-22	-21.5
Diplopoda	10.00	10	9	0	1	0.5
arthropod, unid.	11.00	19	31	-8	-20	-14
Chilopoda	12.00	13	15	-1	-3	-2
Lacertilia	13.00	30	12	-17	1	-8
Gastropoda	14.50	7	13	7.5	1.5	4.5
Diptera	14.50	17	4	-2.5	10.5	4
Insect larvae/pupa	15.00	3	31	12	-16	-2
Acarina	16.00	30	31	-14	-15	-14.5
Thysanura	17.50	30	17.5	-12.5	0	-6.25
Decapoda (crabs)	17.50	30	31	-12.5	-13.5	-13
Lepidoptera larva	19.50	30	17.5	-10.5	2	-4.25
Annelida, undet.	19.50	30	31	-10.5	-11.5	-11
Lepidoptera adults	22.00	30	31	-8	-9	-8.5
Other arachnida	22.00	30	31	-8	-9	-8.5
Pseudoscorpionida	22.00	30	31	-8	-9	-8.5
Apidae	24.00	14	14	10	10	10
Nematoda	24.00	30	31	-6	-7	-6.5
Hirudinea	24.00	21	21	3	3	3

Appendices for Chapter Six

Appendix 6.1. Questionnaire on *Picathartes gymnocephalus*

1. Preliminary information

a. Date b. Name of interviewer

c. Location of interview (district, town, chiefdom, village)

d. Demographic information on interviewee (name, sex, age, tribe, occupation, literacy, duration of residence in area, previous area of residence)

2. Identification and distribution of *Picathartes*

a. What is this? (display picture of *Picathartes*) b. What do you call it here?
c. Have you seen it before?
d. When was the last time you saw it? e. Where did you see it ?
f. Was it alone or in a group when you saw it?
g. In what type of habitat did you see it.?
h. Have you seen this before (display picture of nesting rock with nests) ? Where?
i. Will you take us there?
j. When was the last time you saw some nests?
k. Did you see any eggs or chicks in the nests

3. Social significance and exploitation

a. Have you seen or heard about people catching or killing this bird? If so, when and where?
b. Is this bird important to you or any other people in your area in any way?
c. Would you brush the area around a rock containing the nests of this bird?

Appendix 6.2. Numbers of *Picathartes gymnocephalus* colonies discovered during an extensive survey in Sierra Leone with their activity and reserve status

Region	Site name	Activity status	No. of complete nests	No. of broken nests	Habitat	Reserve status
Gola						
	Jaiboma	Abd	0	2	SF	OR
	Njagor	Act.	3	7	SF	OR
	Tanima	Act.	2	2	SF	OR
	Perrie-B	Act.	1	1	SF	OR
	Lower Koye	Act.	8	0	PF	FR
	Venima-A	Act.	1	0	CP	OR
	Venima-B	Act.	1	0	CP	OR
	Venima-C	Act	1	2	CP	OR
	Baoma-Gaura	Abd	0	3	FB	OR
	Lalehun-DFO:A	Act.	3	5	SF	FR
	Lalehun-DFO:B	Act	3	0	SF	FR
	Belebu-A	Act	1	0	SF	FR
	Belebu-B	Act	2	0	SF	FR
	Maleh	Act	6	8	SF	FR
	Jagbema-A	Act	1	0	SF	FR
	Jagbema-B	Act	1	0	SF	FR
	Jagbema-C	Act	2	0	SF	FR
Kambui Hills						
	Baiama	Act.	7	6	SF	FR
	Komende	Act.	11	11	SF	FR
	Kotumahun-A	Act.	2	0	SF	FR
	Kotumahun-B	Act.	4	0	SF	FR
	Panderu	Act	5	2	SF	FR
	Fabyena(Small Bo)	Abd	0	3	SF	OR
Loma Mts						
	Sk-1	Abd	0	5	SF	FR
	Kon-A	Abd	0	2	SF	FR
	Kon-B	Act.	2	0	SF	FR
	Kania	Abd	0	2	SF	OR
	Sin-A	Act	2	1	SF	OR
	Sin-B	Act	1	2	SF	OR
	Sin-C	Act	1	1	SF	OR
	B/k-A	Act	1	1	SF	OR
	B/k-C	Abd	0	2	FB	OR

Appendix 6.2 (continued)

Kangari Hills						
	Ba-1	Abd	0	1	FB	OR
	Ba-2	Abd	0	1	FB	OR
	Ba-3	Abd	0	1	SF	OR
	Yanieu Hills	Abd	0	3	SF	OR
	Nya-A	Act.	2	6	SF	OR
	Nya-B	Act.	1	1	SF	OR
	Moyogbo	Act.	1	2	FB	OR
	Lomabu-A	Act.	2	4	FB	OR
	Lomabu-B	Abd	0	5	SF	OR
	Kotohun-A	Act	1	2	FB	OR
	Kotohun-B	Abd	1	1	FB	OR
Dodo Hills						
	Baoma IA	Act.	1	2	SF	FR
	Baoma IB	Act.	0	2	SF	FR
	Kpogbu-A	Act.	1	2	SF	FR
	Kpogbu-B	Act.	1	1	SF	FR
	Kpogbu-C	Abd	0	1	SF	FR
	Kpogbu-D	Abd	0	3	FB	FR
	DFO	Abd	0	7	FB	FR
	Baoma-IIA	Abd	0	2	CL	FR
	Baoma-IIB	Abd	0	2	CL	FR
WAPF						
	Malc	Abd	0	1	SF	FR
	Big-water	Act	2	2	PF	FR
	PW	Act.	3	5	SF	FR
	Comfort	Unc.	0	1	SF	FR
	Guma	Unc.	0	1	SF	FR
	HT	Abd	0	1	SF	FR
	Ch-1	Unc.	0	1	SF	FR
	Ch-2	Unc.	0	1	SF	FR

Key:

Abd = abandoned nesting site; Act = active nesting site;

Unc = uncertain activity status

PF = primary forest; SF = secondary forest;

CP = cocoa plantation; CL = cultivated land;

FR = forest reserve; OR = outside reserve

Appendix 6.3: Locations of *Picathartes gymnocephalus* nesting sites discovered during an extensive survey of Sierra Leone

Forest & Grid zone	Site name	Status	No.of nests: Complete	Broken	Geog. coordinates	Map Grid ref UTM	Map sheet number	village
Gola								
29N	Jaiboma	Abd	0	2	7,41N;11.58W	KU 820 500	104	Lalehun
	Njagor	Act.	3	7	7.43N;11,03W	KU 733 541	103	Njagor
	Tanima	Act.	2	2	7.43N;11,03W	KU 740 541	103	Tanima
	Perrie-2b	Act.	1	1	7,38N:11,02W	KU 747 451	103	Jagbwema
	Lower Koye	Act.	8	0	7,38N;10,59W	KU 822 453	104	Lower Koye
	Venima-A	Act.	1	0	7,42N;11,07W	KU 672 508	103	Venima
	Venima-B	Act.	1	0	7,42N;11,07W	KU 675 519	103	
	Venima-C	Act.	1	2	7,42N;11,07W	KU 675 519	103	
	Baoma-Gaura	Abd	0	3	7,44N;11,01W	KU 769 548	103	Baoma
	Lalehun-DFO:A	Act.	3	5	7,41N;11.58W	KU 820 480	104	Lalehun
	Lalehun-DFO:B	Act	3	0	7,41N;11.58W	KU 820 480	104	
	Belebu-A	Act	1	0	7,36N;11.01W	KU 772 402	103	Belebu
	Belebu-B	Act	2	0	7,36N;11.01W	KU 772 402	103	
	Maleh	Act	6	8	7,41N;10,57W	KU 841 489	104	Maleh River
	Jagbema-A	Act	1	0	7,38N;11,01W	KU 440 780	103	Jagbema
	Jagbema-B	Act	1	0	7,38N;11,01W	KU 440 780	103	
	Jagbema-C	Act	2	0	7,38N;11,01W	KU 440 780	103	
Kambui								
29N	Baiama	Act.	7	6	7,49N;11,15W	KU521 669	92	Baiama
	Komende	Act.	11	11	7.53N;11.13W	KU718 558	92	Komende
	Kotumahun-A	Act.	2	0	7,46N;11,15W	KU521 599	92	Kotumahun
	Kotumahun-B	Act.	4	0	7,46N;11,15W	KU521 599	92	
	Panderu	Act	5	2	7.58N;11,09W	KU622 812	92	Panderu
	Fabaina(Small Bo)	Abd	0	3	8,05N; 11.11W	KU604 948	81	Fabaina
Loma Mts								
29P	Sk-1	Abd	0	5	9,13N;11,05W	KA707 188	35	Sukorella
	Kon-A	Abd	0	2	9,09N;11,12W	KA583 117	35	Kondembaia
	Kon-B	Act.	2	0	9,09N;11,12W	KA579 125	35	
	Kania	Abd	0	2	9,12N;11,13W	KA571 170	35	Kania
	Sin-A	Act	2	1	9,13N;11,13W	KA559 188	35	Sinikoro
	Sin-B	Act	1	2	9,13N;11,13W	KA572 212	35	
	Sin-C	Act	1	1	9,14N;11,13W	KA572 208	35	
	B/k-A	Act	1	1	9,18N;11,14W	KA555 278	23	B/karafaia
	B/k-C	Abd	0	2	9,16N;11,14W	KA555 249	23	
	Base camp					KA645 155	35	
Kangari Hills								
29P	Ba-1	Abd	0	1	8,21N;11,42W	KV028 239	67	Bajema
	Ba-2	Abd	0	1	8,21N;11,42W	KV028 239	67	
	Ba-3	Abd	0	1	8,21N;11,42W	KV028 239	67	
	Yanieu Hills	Abd	0	3	8,21N;11,42W	KV018 238	67	
	Nya-A	Act.	2	6	8,22N;11.42W	KV018 254	67	Nyananhun
	Nya-B	Act.	1	1	8,22N;11.42W	KV025 257	67	
	Moyogbo	Act.	1	2	8,24N;11,40W	KV069 300	67	Moyogbo
	Lomabu-A	Act.	2	4	8,21N;11,41W	KV041 235	67	Lomabu
	Lomabu-B	Abd	0	5	8,20N;11,42W	KV038 229	67	
	Kotohun-A	Act	1	2	8,23N;11,41W	KV035 278	67	Kotohun
	Kotohun-B	Act	1	1	8,23N;11,42W	KV029 275	67	

Appendix 6.3. (cont).

Dodo								
	Baoma IA	Act.	1	2				Baoma I
	Baoma IB	Act.	0	2				
	Kpogbu-A	Act.	1	2				Kpogbu
	Kpogbu-B	Act.	1	1				
	Kpogbu-C	Abd	0	1				
	Kpogbu-D	Abd	0	3				
	DFO	Abd	0	7				DFO Camp
	Baoma-IIA	Abd	0	2				Baoma II
	Baoma-IIB	Abd	0	2				
WAPF	Malc	Abd	0	1	8,21N;13,19W	005 232	Sp.sheet	No.2
	Big-water	Act	2	2	8,19N;13,11W	043 192	Sp.sheet	Big water
	PW	Act.	3	5	8,21N;13,19W	998 235	Sp.sheet	No.2
	Comfort	Unc.	0	1	8,20N; 13,10W	017 205	Sp.sheet	Tokeh
	Guma	Unc.	0	1	8,23N;13,17W	953 278	Sp.sheet	Mile 13
	HT	Abd	0	1	8,21N;13,19W	998 230	Sp.sheet	No.2
	CH-1	Unc.	0	1	8,25N;13,18W	980 304	Sp.sheet	Charlotte
	CH-2	Unc.	0	1	8,25N;13,18W	979 302	Sp.sheet	Charlotte

Sp sheet = special sheet; Abd = abandoned; Act = Active; Unc = uncertain status

Missing data not available

Appendix 6.4: locations of villages visited during the extensive survey at which no *Picathartes* colonies known

Region	Village visited	Position Geog. coordinates	Map Grid ref UTM	Grid Zone	Map sheet number
Gola We	Nemahugoima	7,25N;11,24W	KU505 200	29N	111
	Pewa	7,21N;11,22W	KU465 138	29N	111
	Toyema	7,25N;11,20W	KU428 203	29N	111
	Samatia	7,25N;11,20W	KU421 199	29N	111
	Golawoma	7,29N;11,20W	KU431 235	29N	111
	Palima	7,20N;11,22W	KU455 116	29N	111
	Bunumbu	7,27N;11,21W	KU408 238	29N	111
	Bindalahun	7,26N;11,16W	KU531 225	29N	112
Gola Noı	Patama	7,43N;10,54W	KU913 525	29N	104
	Bandajuma	7,43N; 10,52W	KU 952 529	29N	104
	Joru	7,42N;11,03W	KU732 508	29N	103
	Nyandehun	7,47N;10,56W	KU868 598	29N	93
Kambui	Fonima	8,00N;11,15w	KU518 843	29N	91
	Nyandehun	7,43N;11,22W	KU397 542	29N	102
	Serabu	7,51N;11,17W	KU478 688	29N	91
	Bambawo	8,01N;11,08W	KU650 860	29P	81
	Dia Nog	7,51N;11,16W	KU499 765	29N	91
	Gengeru	7,54N;11,17W	KU552 729	29N	92
	Kamboiwabu	7,50N;11,13W	KU557 668	29N	102
	Lago	7,41N;11,20W	Ku432 504	29n	102
	Koyagbwema	7,50N;11,12W	Ku568 669	29N	92
	Lomabu	7,53N;11,15W	KU525 715	29N	92
	Kpai	7,51N;11,15W	KU519 688	29N	91
	Taninihun	7,52N;11,15W	KU512 699	29N	91
	Deamei	7,49N;11,13W	KU550 647	29N	92
	Wanjaima	7,51N;11,16W	KU504 684	29N	91
	Kagbwama	7,58N;11,13W	KU552 819	29N	92
	Tokpwadi	7,41N;11,24W	KU499 499	29N	102
	Fuya	7,58N;11,08W	Ku642 819	29N	92
	Menema	7,40N;11,20W	KU418 484	'29N	102
	Jai	7,39N;11,22W	KU461 462	29N	102
	Waiama	7,52N;11,22W	Ku462 708	29N	91
	Hangha	7,57N;11,08W	KU640 782	29N	92
	Tinehun	7,57N;11,14W	KU541 797	29N	92
	Menema-Dia	7,56N;11,16W	KU508 754	29N	91
	Jenne	7,35N;11,21W	Ku414 384	29N	92
	Konjo	7,55N;11,16W	KU508 754	29N	91
	Njala	7,49N;11,17W	KU485 651	29N	91
	Tiso	7'55N;11,11W	KU621 759	29N	92

Appendix 6.4 (cont)

Loma M	Gambafaia	9,08N;11,13W	KA562 106	29P	35
	Bandankoro	9,17N;11,04W	KA731 285	29P	23
	Keimadugu	9,19N;11,09W	KA645 300	29P	23
	Pirankoro	9,03N;11,12W	KA575 019	29P	35
	Mansonia	9,08N;11,05W	KA710 099	29P	35
Kangari	Masaba	8,34N;11,40W	KV071 482	29P	56
Hills	Ro-sul	8,33N;11,41W	KV045 462	29P	56
	Ro-fothane	8,33N;11,41W	KV045 466	29P	56
	Gbon-Jalloh	8,32N;11,42W	KV043 441	29P	56
	Gbon-Kamara	8,32N;11,42W	KV042 442	29P	56
	Makoth	8,30N;11,42W	KV035 411	29P	56
	Mante mabi	8,29N;11 14W	KV048 378	29P	67
	Bukosir	8,30N;1,39W	KV078 403	29P	67
	Kiarafay	8,33N;11,41W	KV050 455	29P	67
	Rogbara	8,34N;11,41W	KV041 478	29P	56
	Rowalla	8,33N;11,41W	KV052 465	29P	56
Kasewe	Kasewe(Kori)	8,19N;12,17W	HE017 243	28P	65
	Masheriffu(Yoni)	8,21N;12,10W	HE121 239	28P	65
	Gbonkolaa(Yoni)	8,22N;12 10W	HE112 258	28P	65
	Rotench(Yoni)	8,24N;12,09W	HE108 294	28P	65
	Malenpe(Yoni)	8,23N;12,09W	HE091 298	28P	65
	Bonkababe(Yoni)	8,21N;12,13N	HE072 243	28P	65
	Moyamba ow(Yoni)	8,20N;12,12W	HE080 220	28P	65
	Moyamba junction(Kori)	8,01N;12,04W			
	Makundi	8,19N;12,10W	HE124 209	28P	65
WAPF	Goderich	8,26N;13,17W	894 311		Sp sheet
	Hamilton	8,23N;13,15W	922 235		Sp sheet
	No. 2	8,21N;13,19W	020 232		Sp sheet
	Tokeh	8,20N;13,10W	017 205		Sp sheet
	Regent	8,26N;13,12W	030 330		Sp sheet
	John O-bay	8,15N;13, 10W	035 120		Sp sheet

Appendix 6.5. Habitat characteristics of *Picathartes gymnocephalus* nesting sites in forest

Nesting sites	Tree density Nos/ha	Basal area sq.m/ha	Canopy cover (%)	Canopy height (m)	Hill slope (m)	Distance to water-course (km)	Distance to edge (km)
Gola							
LKR	560	69.8	63.9	13.2	34	0.25	2
DFO-a	773.3	71.21	71.7	14.9	30	1.5	
Maleh	813.2	113.8	70.7	17.6	12	0.25	
UKR-a	1200	195.4	68.3	16	65	0.03	
UKR-b	686.6	128.9	87.3	13.3	46	0.05	
DFO-b	1093	166.6	68.2	16	47		
Tanima	26.44	6.4			30	0.005	0.04
Njagor	206.6	20.3	78.8	17.7	44	2	0.05
Belebu	859.2	198.5	71.9	13.3	28.5	2	0.001
Perrie	606.6	82.3	85.1	21	10	0.1	0.03
WAPF							
No2	420	40.5	83.3	13.9	34.9	0.02	1.5
JOB-1	226.6	26.98	71.6	10.5	39.8	0.1	2
JOB-2	286.6	68.1	75.2	20.3	28.9	0.025	2
JOB-3	353.4	24.8	79.8	16.5	34.3	0.025	1
BJ	245	65.8	80	16.5		0.372	
Bennet	620	38.2	60	13.6	7.5	0.02	
Ngoboh	575	41.1	70	13.3		0.4	
Kambui							
Komende	420	112.4	60.8	17.7		0.25	0.07
Baiama	500	105.5	75.4	17.5	17.5	0	0.005
Dodo							
Kpogbu-a	140	99.3	56	13	24		
Kpogbu-b	20	0.41					

Missing values indicate data not recorded due either to rough terrain, lack of time or in the case of clearings, none seen.

Appendix 6.6: Distribution of *P. gymnocephalus* nests on nesting rocks

Region	Nesting site	No. of nests	No. of rock faces	Nest No.	Height above ground (cı	Distance to nearest nest (cm)
Gola forest	UKR A		6	1	1	54.5
				2	180	54.5
				3	148.5	121
				4	219	110
				5	189	185
				6		
	UKRB	2	1	1	173.4	207
				2	285	207
	La1	4	2	1	200	
				2	325	90
				3	300	90
				4	200	90
	La2	3	2	1	257.5	1000
				2	205.5	1000
				3	242.7	
	Maleh	7	2	1	391	
				2	305.8	73.5
				3	650	
				4	200	113.2
				5	289	125
				6	297	
				7	404	
	LKR	2	2	1	157	
				2	153.5	63.8
				3	203.8	63.8
	Tanima	3	1	1	182	145
				2	241	145
	Njagor	4	2	1	227	90
				2	200	65
	Belebu	2	1	1	192	84
				1	257	84
	Perrie	2	1	1	200	
				2	180	
	Venima	1	1	1	155	
Kambui	Baiama	7	1	1	190	112
				2	139	112
				3	161	213
				4	200	288

Appendix 6.6 (cont)
Kambui Hills (cont)

				5	315	118
				6	273	118
				7	324.7	118
	Komende	11	2	1	168	147
				2	241	147
				3	179	113
				4	147	74
				5	188	67.5
				6	204	76
				7	245	70
Loma mts	Kon-A	2	1	1	168	
				2	243.8	
	Kon-B	2	2	1	290	
				2	204	
	Sin-A	2	1	1	223	
				2	188	
	Sin-B	1	1	1	220	
	Sin-C	1	1	1	161	78
	B/K-A	1	1	1	243	
Kamgari	Nya-A	2	1	1	312	200
				2	512	200
	Nya-B	1	1	1	215	
	Moyogbo	1	1	1	155	
	Lomabu-A	2	1	1	124	23
				2	155	87.8
	Kotohun-A	1	1	1	152	
	Kotohun-B	1	1	1	297	
Dodo	Baoma-A	1	1	1	139	
	Kpogbu-A	1	1	1	187	
	Kpogbu-B	1	1	1	104	100
WAPF	J-O-B:3	1	1 (4)	1	366	
	J-O-B:2	1	1	1	340	
	J-O-B:1	2	1(2)	1	300	50
				2	380	50
	J-O-B:4	1	1	1	320	
	BJ	1	1	1	320	
	Ngbonohk	1	1	1	125	
	Bennet1	1	1	1	250	
	Bennet2	1	1	1	246	
	No.2	1	1	1	212	

Missing data not recorded due to iinaccessibility or rough terrain
Numbers of nests and numbers of measuremnents given may not correspond because of missing data

Appendix 6.7:The ecological characteristics of *P. gymnocephalus* nesting rocks in different regions of Sierra Leone

Region	Site	No. of nests per site	No. of rock faces with nests	Rock face height (m)	Rock face width (m)	Rock face area (sq.m)	Rock face slope (degrees)	No. of complete nests per rock face
Gola	UKR-A	6	1	13.5	13.5	182.25	90	6
Forest	UKR-B	2	1	7.452	6.3	46.9476	35	2
	Lalehun-A	1	1	15.5	4.78	74.09	67	1
	Lalehun-B	2	2	18	4.466	80.388	40	1
				18	2.62	47.16	56	1
	LKR	4	2	7	3.14	21.98	58	1
				10	4.95	49.5	66	3
	Maleh	7	2	6.5	3.5	22.75	27	3
				11	5.2	57.2	32	3
	Tanima	3	1	3.5	9	31.5	16	3
	Njagor	4	2	3	6.15	18.45	36	3
				4.5	3	13.5	30	1
	Belebu	2	1	11	18.6	204.6	60	1
	Perrie	2	1	14.5	14.3	207.35	40	1
	Venima:B	1	1	4.2	23	96.6	34	1
Kambui	Baiama	7	1	5.48	15.38	84.2824	24	7
Hills	Komende	11	3	2.25	5.57	12.5325	90	2
				2.18	7.29	15.8922	62	5
				3.22	7.895	25.4219	62	4
Loma	K/baia-A	2	1	7.2	50	360	5	2
Mts	K/baia-B	2	2	6	20	120	90	1
				6	5	30	20	1
	S/koro-A	2	2	5	3.5	17.5	60	1
				3	3.01	9.03	45	1
	S/koro-B	1	1	9.14	9.14	83.5396	25	1
	S/koro-C	1	1	4.95	4.5	22.275	10	1
	B-K/faia	1	1	4	5.25	21	80	1
Kangari	N/hun : A	2	1	3.33	7.65	25.4745	73.5	2
Hills	N/hun:B	1	1	6.61	9	59.49	44	1
	Moyogbo	1	1	7.48	5.145	38.4846	24	1
	Lomabu	2	1	3.66	5.332	19.5151	49	1
	Kotohun:A	1	1	2.7	11.6	31.32	54	1
	Kotohun:B	1	1	4.03	10.78	43.4434	40	1
Dodo	Baoma	1	1	7.17	2.3	16.491	30	1
Hills	Kpogbu:A	1	1	4.55	20.27	92.2285	36	1
	Kpogbu:B	1	1	2.6	19.5	50.7	28	1
WAPF	J-O-B:1	2	1	13.5	4.2	56.7	16	2
	J-O-B:2	1	1	2.5	9.24	23.1	40	1
	J-O-B:3	1	1	9.45	1.05	9.9225	10	1
	bj1	2	1	12	5	60	30	1
	Ngo	1	1	3.85	2.25	8.6625	40	1
	bennet	1	1	6.7	10.7	71.69	20	1
	No2	2	1	7.35	16.05	117.968	52.5	2

Appendix 6.8. Relation between the distribution of *Picathartes gymnocephalus* nesting sites on the WAPF and landform factors

Map grid no.	No. of nesting sites	No. of active nests	Total no of nests	No. of contours	Mean altitude	River length
			0	0	4	227.3	5.3
2	2	6	7	439.4	2.35
2.1	0	0	8	467.5	4.55
3	1	2	8	323.2	5.35
4	0	0	10	515.15	3.575
5	3	3	9	527.3	1.05
8	0	1	9	363.6	4.2
10	0	0	9	373.7	1.5
14	0	1	7	428.6	1.925
15	1	5	6	272.7	3.95
15.1	0	0	5	181.5	8.4
16	0	1	9	424.2	2.7
18	3	3	8	597.4	0.55
18.1	2	3	6	318.2	2.05
20	0	0	4	354.6	4.3

Appendices for Chapter Seven

Appendix 7.1. Species selected for phylogenetic analysis as putative relatives of *Picathartes*. Taxa arranged in order of data input. Traditional classification used (Howard and Moore, 1991) with families from Sibley and Munroe (1990) in brackets where differences occur.

Species	Code name for data input (key to Appendices 7.2 & 7.3)	English name	Family	Distribution
1. *Lanius ludovicianus*	L.ludov_x	Loggerhead Shrike	Laniidae	North & Central America
2. *Orthonyx spaldingi*	O.spald_x	Northern Logrunner	Orthonychidae	Australia
3. *Turdus cardis*	Turdus.c_x	Japanese Grey Thrush	Turdidae	Asia
4. *Zoothera lunulata*	Z.lun_x	Olive-tailed thrush	Turdidae	Australia
5. *Acrocephalus schoenobaenus*	ac.schoe_x	Sedge warbler	Sylviidae	Europe, Asia; Africa
6. *Aphelocoma coerulescens*	ap.coer_x	Scrub Jay	Corvidae	North America
7. *Catharus guttatus*	ca.gut_x	Hermit Thrush	Turdidae	Central & North America
8. *Cettia diphone*	ce.diphone_x	Japanese Bush Warbler	Sylviidae	Asia
9. *Cissa chinensis*	ci.chin_x	Green Magpie	Corvidae	Southeast Asia
10. *Cincinnurus regius*	cin.cin_x	King Bird-of-paradise	Paradisaeidae	New Guinea
11. *Corvus corax*	cor.c_x	Common Raven	Corvidae	Europe, Asia, North Africa
12. *Cyclarhis gujanensis*	cyclar.g_x	Rufous-browed Peppershrike	Vireonidae	Central & South America
13. *Erithacus rubecula*	erith.r_x	European Robin	Turdidae	Europe, Asia & North Africa
14. *Ficedula narcissina*	fice.n_x	Narcissus Flycatcher	Muscicapidae	East Asia
15. *Laniarius turatiii*	lani.t_x	Turatii's Boubou	Laniidae	W. Africa:Senegal-Sierra Leone
16. *Leiothrix lutea*	lei.lut_x	Red-billed Leiothrix	Timaliidae	Asia

Appendix 7.1. (cont).

17. *Monticola solitarius*	mon.s_x	Blue Rock Thrush	Turdidae	Europe, Asia & Africa
18. *Pomatostomus isidori*	p.isid_x	Rufous Babbler	Timaliidae (Pomatostomidae)	Australia
19. *Parus major*	pa.major_x	Great Tit	Paridae	Europe, Asia, N. Africa
20. *Paradisaea minor*	para.min_x	Lesser Bird-of-paradise	Paradisaeidae	New Guinea
21. *Phylloscopus sibilatrix*	ph.sibil_x	Wood Warbler	Sylviidae	Europe > Central Africa
22. *Picathartes oreas*	pic.e_x	Grey-necked Picathartes	Picathartidae	W. Africa: Nigeria-Gabon
23. *Ptilostomus afer*	ptil.afer	PiaPiac	Corvidae	Africa
24. *Pyrrhocorax pyrrhocorax*	py.pyr_x	Common Chough	Corvidae	Asia, Africa & Europe
25. *Regulus satrapa*	r.satrap_x	Golden-crowned Kinglet	Sylviidae (Regulidae)	North & Central America
26. *Sturnus cineraceus*	sturn.c_x	Grey Starling	Sturnidae	Asia
27. *Sylvia atricapilla*	sylvia.a_x	Blackcap	Sylviidae	Europe, Asia>Africa
28. *Vireo olivaceus*	vi.oliv_x	Red-eyed Vireo	Vireonidae	N & S. America, Caribbean
29. *Vireolanius leucotis*	vr.leuc_x	Slaty-capped Vireo	Vireonidae	Central & South. America
30. *Zosterops japonica*	zo.japon_x	Japanese White-eye	Zosteropidae	Japan

Appendix 7.2. Part of the ECLUSTALW alignment of DNA sequences of part of the cytochrome *b* gene from *Picarthartes oreas* and 29 putative relative species (positions 201-250).

Picathartes oreas	ATGCAAACGG AGCTTCCTTA TTCTTCATCT GCATCTACAT CCACATTGGC
Lanius ludovicianus	ATGCAAACGG AGCCTCATTT TTCTTCATTT GCATCTACCT ACATATCGGC
Orthonyx spaldingi	ACGCAAACGG AGCCTCCCTA TTCTTCATCT GCATTTACAT TCACATCGGC
Turdus cardis	ACGCAAACGG AGCCTCACTA TTCTTTGTCT GCATCTATCT ACACATTGGC
Zoothera lunulata	ACGCAAACGG AGCCTCATTC TTCTTTATCT GCATCTACCT TCACATTGGA
Acrocephalus schoebaenus	ACGCAAACGG GGCTTCCTTC TTCTTCATCT GCATCTACTT CCACATCGGC
Aphelocoma coerulescens	ATGCAAACGG AGCTTCCTTC TTCTTCATCT GTATTTACTT ACATATCGGC
Catharus guttatus	ATGCAAACGG AGCCTCATTC TTCTTCATCT GCATCTACCT CCACATCGGC
Cettia diphone	ACGCAAACGG AGCTTCCTTC TTCTTTATCT GCATTTACTT CCACATTGGC
Cissa chinensis	ATGCAAACGG GGCCTCATTC TTCTTCATCT GCATCTACCT ACACATCGGC
Cincinnurus regius	ATGCAAACGG AGCTTCCTTA TTTTTTATTT GCATCTACCT ACACATCGGC
Corvus corax	ACGCAAATGG AGCCTCTTTC TTCTTCATTT GCATCTACTT ACACATCGGC
Cyclarhis gujanensis	ACGCAAACGG GGCCTCATTC TTCTTCATCT GCATCTACCT ACACATCGGC
Erithacus rubecula	ATGCAAACGG AGCCTCATTC TTCTTCATCT GCATCTACCT CCACATCGGC
Ficedula narcissina	ACGCAAACGG AGCCTCTTTC TTCTTTATTT GCATCTACCT GCACATTGGC
Laniarius turatii	ACGCAAACGG AGCTTCCCTA TTCTTTATCT GCATCTACCT ACACATTGGA
Leiothrix lutea	ATGCGAACGG AGCCTCATTC TTCTTCATTT GCATCTACTT CCACATCGGC
Monticola solitarius	ATGCAAACGG AGCCTCATTC TTCTTCATCT GCATCTATCT ACACATCGGC
Pomatostomus isidori	ATGCCAACGG AGCCTCACTC TTCTTCATCT GCATCTATCT ACACATCGGA
Parus major	ACGCAAACGG AGCCTCCTTC TTCTTCATCT GCATCTACTT CCACATCGGT
Paradisaea minor	ATGCAAACGG AGCTTCCTTA TTCTTTATTT GCATCTACCT ACACATCGGC
Phylloscopus sibilatrix	ACGCAAACGG AGCCTCCTTC TTTTTCATCT GCATTTACCT ACATATCGGA
Ptilostomus afer	ATGCAAACGG AGCCTCCTTC TTCTTCATCT GCATCTACCT ACATATCGGC
Pyrrhocorax pyrrhocorax	ACGCAAACGG AGCCTCCTTC TTCTTCATTT GCATCTACCT CCACATTGGC
Regulus satrapa	TAGCATTAAT AGCAACTGCC TTCGTAGGCT ACGTCCTACC TTGAGGACAA
Sturnus cineraceus	ACGCAAACGG AGCATCATTC TTTTTCATCT GCATCTACCT ACACATCGGA

Appendix 7.2 (cont).

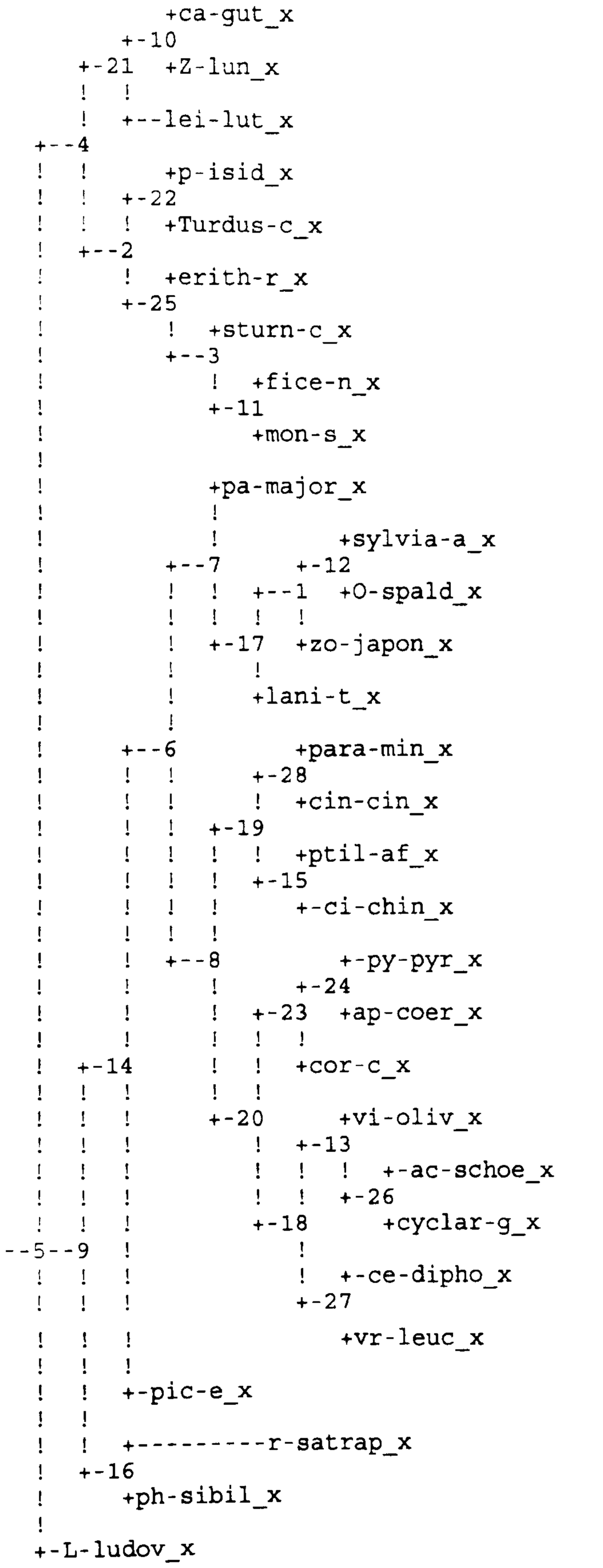
Sylvia atricapilla	ACGCAAACGG AGCTTCATTC TTCTTCATCT GCATCTACAT TCACATTGGC
Vireo olivaceus	ACGCAAACGG AGCCTCCTTN TTCTTTATCT GCATCTACCT TCACATCGGC
Vireolanius leucotis	ACGCAAACGG AGCCTCTTTT TTCTTCATCT GCATTTACCT ACATATCGGC
Zosterops japonica	ACGCAAACGG AGCCTCCTTC TTCTTCATCT GCATCTACCT ACACATCGGC

Appendix 7.3a. Approximate confidence limits of Maximum Likelihood phylogenetic tree shown in Figure 7.3 (Chapter 7) of *P. gymnocephalus* and 29 putative relatives (see Appendix 7.3b for key to branch nodes).

Between	And	Length	Approx. Confidence Limits		
5	L-ludov_x	0.03885	(0.02653,	0.05124)	**
5	4	0.00123	(zero,	0.00396)	
4	21	0.00668	(0.00110,	0.01230)	**
21	10	0.00312	(zero,	0.00816)	
10	ca-gut_x	0.01502	(0.00730,	0.02272)	**
10	Z-lun_x	0.02446	(0.01452,	0.03448)	**
21	lei-lut_x	0.03696	(0.02318,	0.05069)	**
4	2	0.00293	(zero,	0.00686)	**
2	22	0.00784	(0.00108,	0.01454)	**
22	p-isid_x	0.02086	(0.00979,	0.03192)	**
22	Turdus-c_x	0.02599	(0.01450,	0.03741)	**
2	25	0.00010	(zero,	0.00446)	
25	erith-r_x	0.01151	(0.00454,	0.01856)	**
25	3	0.00626	(0.00050,	0.01203)	**
3	sturn-c_x	0.01599	(0.00713,	0.02480)	**
3	11	0.00323	(zero,	0.00769)	*
11	fice-n_x	0.02527	(0.01415,	0.03639)	**
11	mon-s_x	0.01005	(0.00289,	0.01722)	**
5	9	0.00227	(zero,	0.00545)	**
9	14	0.00064	(zero,	0.00260)	
14	6	0.00468	(0.00014,	0.00920)	**
6	7	0.00316	(zero,	0.00789)	
7	pa-major_x	0.02125	(0.01100,	0.03140)	**
7	17	0.00438	(zero,	0.00962)	**
17	1	0.00276	(zero,	0.00812)	
1	12	0.01077	(0.00298,	0.01855)	**
12	sylvia-a_x	0.02542	(0.01454,	0.03633)	**
12	O-spald_x	0.02853	(0.01620,	0.04091)	**
1	zo-japon_x	0.01771	(0.00832,	0.02720)	**
17	lani-t_x	0.02257	(0.01241,	0.03270)	**
6	8	0.00467	(0.00036,	0.00900)	**
8	19	0.00345	(zero,	0.00751)	**
19	28	0.01745	(0.00902,	0.02586)	**
28	para-min_x	0.01694	(0.00876,	0.02509)	**
28	cin-cin_x	0.00613	(0.00080,	0.01146)	**
19	15	0.00544	(zero,	0.01090)	**
15	ptil-af_x	0.01591	(0.00768,	0.02411)	**
15	ci-chin_x	0.02701	(0.01648,	0.03759)	**
8	20	0.00107	(zero,	0.00322)	
20	23	0.00301	(zero,	0.00696)	**
23	24	0.00239	(zero,	0.00634)	
24	py-pyr_x	0.02566	(0.01545,	0.03589)	**
24	ap-coer_x	0.02076	(0.01170,	0.02981)	**
23	cor-c_x	0.01621	(0.00824,	0.02424)	**
20	18	0.00262	(zero,	0.00618)	**
18	13	0.00216	(zero,	0.00529)	**
13	vi-oliv_x	0.01792	(0.00954,	0.02619)	**
13	26	0.00506	(0.00004,	0.01009)	**
26	ac-schoe_x	0.02110	(0.01171,	0.03042)	**
26	cyclar-g_x	0.01456	(0.00611,	0.02307)	**
18	27	0.00577	(0.00004,	0.01149)	**
27	ce-dipho_x	0.02174	(0.01127,	0.03213)	**
27	vr-leuc_x	0.01446	(0.00593,	0.02298)	**
14	pic-e_x	0.02317	(0.01348,	0.03279)	**
9	16	0.00652	(zero,	0.01449)	*
16	r-satrap_x	0.18185	(0.14248,	0.22123)	**
16	ph-sibil_x	0.01982	(0.00985,	0.02971)	**

* = significantly positive, P < 0.05
** = significantly positive, P < 0.01

Appendix 7.3b. Key to branch nodes in Appendix 7.3a.



Appendix 7.4a. Approximate confidence limits of Maximum Likelihood Phylogenetic tree shown in Figure 7.4 (Chapter 7) of *P. gymnocephalus* and 29 putative relatives (see Appendix 7.4b for key to branch nodes).

between	and	Length	Approx. Confidence Limits	
20	L-ludov_x	0.03096	(0.01966,	0.04227) **
20	2	0.00731	(0.00115,	0.01354) **
2	19	0.00434	(zero,	0.00930) **
19	zo-japon_x	0.02168	(0.01132,	0.03204) **
19	10	0.00171	(zero,	0.00616)
10	21	0.00620	(0.00022,	0.01219) **
21	sylvia-a_x	0.03249	(0.02039,	0.04460) **
21	pa-major_x	0.01588	(0.00664,	0.02512) **
10	lani-t_x	0.02126	(0.01144,	0.03108) **
2	8	0.00396	(zero,	0.00826) **
8	3	0.00435	(0.00013,	0.00859) **
3	16	0.00359	(zero,	0.00770) **
16	27	0.01804	(0.00940,	0.02672) **
27	para-min_x	0.01659	(0.00843,	0.02475) **
27	cin-cin_x	0.00665	(0.00105,	0.01232) **
16	4	0.00510	(zero,	0.01039) **
4	ptil-af_x	0.01562	(0.00736,	0.02366) **
4	ci-chin_x	0.02717	(0.01655,	0.03785) **
3	13	0.00084	(zero,	0.00292)
13	6	0.00452	(zero,	0.00915) **
6	cor-c_x	0.01368	(0.00622,	0.02125) **
6	ap-coer_x	0.02209	(0.01277,	0.03147) **
13	22	0.00324	(zero,	0.00728) **
22	25	0.00247	(zero,	0.00592) **
25	7	0.00472	(zero,	0.00961) **
7	ac-schoe_x	0.02119	(0.01173,	0.03059) **
7	cyclar-g_x	0.01466	(0.00618,	0.02325) **
25	vi-oliv_x	0.01827	(0.00983,	0.02670) **
22	14	0.00570	(zero,	0.01142) **
14	vr-leuc_x	0.01437	(0.00587,	0.02285) **
14	ce-dipho_x	0.02174	(0.01127,	0.03221) **
8	28	0.00414	(zero,	0.00835) **
28	26	0.00493	(zero,	0.01018) **
26	O-spald_x	0.03209	(0.01928,	0.04488) **
26	pic-e_x	0.01943	(0.01027,	0.02862) **
28	5	0.00066	(zero,	0.00293)
5	23	0.00623	(zero,	0.01424)
23	r-satrap_x	0.19232	(0.14925,	0.23533) **
23	ph-sibil_x	0.01993	(0.00992,	0.02994) **
5	1	0.00626	(0.00119,	0.01128) **
1	12	0.00006	(zero,	0.00367)
12	17	0.00291	(zero,	0.00689) **
17	18	0.00710	(0.00117,	0.01299) **
18	24	0.00151	(zero,	0.00617)
24	ca-gut_x	0.01407	(0.00642,	0.02170) **
24	lei-lut_x	0.04024	(0.02564,	0.05474) **
18	Z-lun_x	0.02453	(0.01448,	0.03457) **
17	15	0.00322	(zero,	0.00821) *
15	9	0.00314	(zero,	0.00765) *
9	sturn-c_x	0.01668	(0.00747,	0.02581) **
9	mon-s_x	0.01122	(0.00372,	0.01884) **
15	fice-n_x	0.02579	(0.01444,	0.03704) **
12	11	0.00777	(0.00106,	0.01448) **
11	p-isid_x	0.02172	(0.01030,	0.03316) **
11	Turdus-c_x	0.02530	(0.01384,	0.03665) **
1	erith-r_x	0.01290	(0.00546,	0.02036) **
20	py-pyr_x	0.02226	(0.01254,	0.03201) **

* = significantly positive, P < 0.05
** = significantly positive, P < 0.01

Appendix 7.4b. Key to branch nodes in Appendix 7.4a